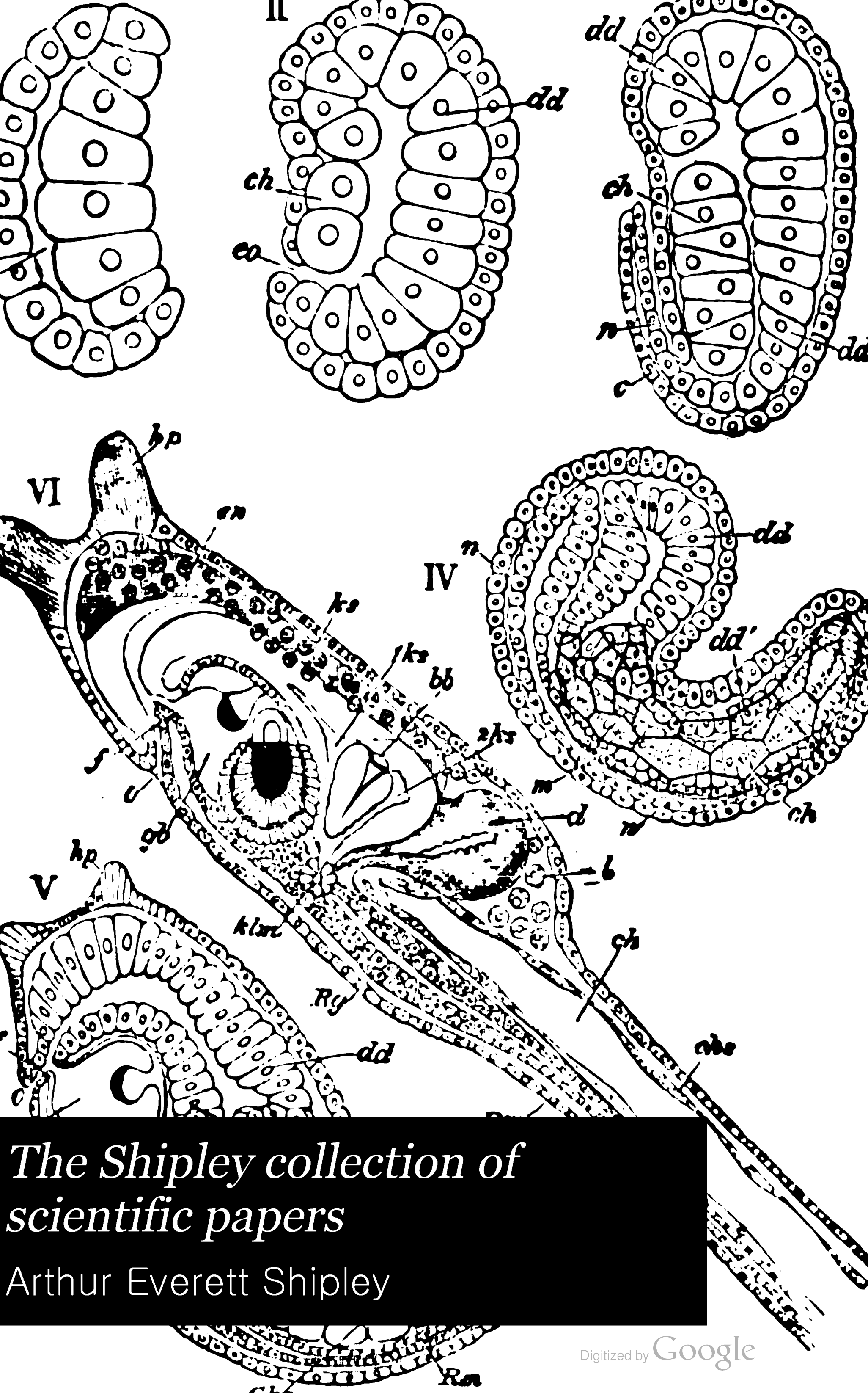
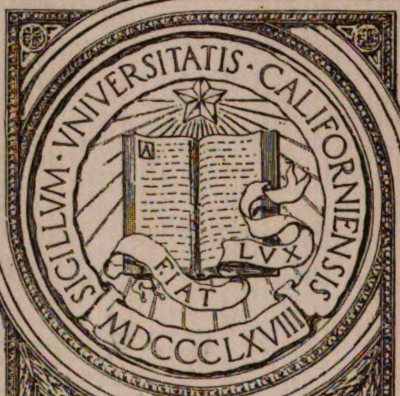


The Shipley collection of scientific papers

Arthur Everett Shipley


SIGILLVM · VNIVERSITATIS · CALIFORNIENSIS
FIAT LVX
MDCCCLXVIII

Turner (Sir W.) The cell theory, past and present.

MacBride (E.W.) Sedgwick's theory of the Embryonic Phase of Ontogeny.

Sedgwick (A.) On the origin of metameric segmentation.

Bourne (G.C.) A criticism of the Cell-Theory.

Davenport (C.B.) & Bullard (C.) Studies in Morphogenesis. VI.

Weldon (W.F.R.) ~~Ext~~. An attempt to measure the death-rate due to the selective destruction of Carcinus maenas.

" . Remarks on variation in animals and plants.

Ewart (J.C.) Telegony experiments: The birth of a hybrid between a male Burchell's zebra (E.B) & a mare (E.C.)

Spencer (H.) Weismannism once more.

" . A rejoinder to Prof. Weismann.

Weismann (A.) The all-sufficiency of natural selection. I.

" " II.

Monckman (Dr.) Science at Cambridge.

Wallace (A.R.) The method of organic evolution. I.

Mac Bride (E.W.) The position of morphology in zoological science.

(*With the Author's compliments.*)

to Mr. Shipley

THE CELL THEORY, PAST AND PRESENT:

BEING THE

INAUGURAL ADDRESS

DELIVERED NOVEMBER 1, 1889,

TO THE

SCOTTISH MICROSCOPICAL SOCIETY.

BY

SIR WILLIAM TURNER, KNT.,

M.B., LL.D., D.C.L., F.R.SS. L. AND E.,

PRESIDENT OF THE SOCIETY.

EDINBURGH:

PRINTED BY NEILL AND COMPANY.

1890.

THE CELL THEORY, PAST AND PRESENT.

GENTLEMEN,

In taking the Chair at the First General Meeting of the Scottish Microscopical Society, I would offer to the members my hearty thanks for having done me the honour to choose me as the President under whom the work of the Society is to be inaugurated, and during whose incumbency the Society is to begin to substantiate its claim to have an existence amongst the scientific societies in Scotland. I cannot but think that I owe this honour to a friendly feeling entertained towards me personally by the members, so many of whom I can claim as old pupils, rather than to the special work that I have done in research with the microscope. For although I have been accustomed to use the instrument as an aid to my anatomical studies, yet my attention, more especially of late years, has not been so continuously directed to inquiries in which the microscope is an essential instrument, as has been the case with other members of the Society, who from having specialised their work are more entitled to your confidence.

In making our first public appearance as a Society it will be advisable that I should say a few words in support of our existence, and of the reason why those who have been mainly instrumental in founding the Society have considered that such an association might fill a vacant place and discharge a useful function in this division of the kingdom. The primary object of the Society is to bring into closer communication with each other all who are interested in the use of the microscope, and who are engaged in researches in which this instrument is a necessity. As the employment of the microscope is not limited to any single branch of science, the Society is intended to include persons interested in every department of knowledge in which the instrument is or can be employed. We shall be glad to hear communications on the optical principles which guide the maker in the construction and improvement of lenses. We shall welcome into our body those who are engaged in the manufacture of the instrument and its various appliances, especially if they will communicate to our Proceedings the particulars of improvements in it, or in any of its associated apparatus. We shall be delighted to receive communications on new and better methods of preparing and displaying specimens, so that they may be examined with more exactitude. All advances in microscopic technique will be welcomed by us.

But we must not stop here. Improvements in the instrument are not the main end and object of our existence. Our great duty is to advance those sciences in which the instrument is employed; to probe to their very depths the secret places of nature, and to do our best to advance knowledge. We shall have to inquire into the structure of plants and animals in conditions both of health and disease—to investigate the changes which take place in them in connection with the discharge of their respective functions. Those of our members who are engaged in geological and mineralogical studies will doubtless communicate to us the result of their researches into the microscopic structure of rocks and minerals, and the form of their constituent crystals. Manufacturers of textile fabrics may also have something to say on the economic applications of the instrument; whilst those who take a delight in testing the powers of their objectives can bring before us any new object, the markings on which their instruments are capable of resolving, and which may furnish perhaps a more satisfactory test of accuracy of definition than any we had previously possessed.

But while the advance of science is our prime function, there are others which, we believe, will not be without benefit to our members. We do not propose that our meetings should be entirely occupied, as is the case with some of the older societies, with the formal reading of papers. We wish to encourage the exhibition of specimens, and to have discussion on them, so as to promote an interchange of views as to the meaning of the appearances presented by the objects exhibited. Observers will then have an opportunity of testing and comparing each other's work, they will be benefited by mutual criticism, and stimulated to further labours. Should our Society prosper and attract a large membership, we hope to be provided with funds, by means of which we may render assistance to our members in the preparation of their researches for publication. One direction in particular, in which I think we may profitably employ our surplus funds, if any, is to make advances to assist in the illustration of the papers communicated to our Society. All who have been engaged in the publication of scientific memoirs know the difficulty of obtaining adequate illustration of their work on account of the expense attendant on it. I understand also that the Council have in contemplation the preparation, for the use of members, of a classified catalogue of memoirs and books, descriptive of objects that have been studied with the use of the microscope.

In developing our work, we are to keep in mind that the microscope is only an instrument and is not the science, that its use can only be empirical if the user has not made himself acquainted, to some extent at least, with the principles of the science, for the investigation of which the instrument is employed, and that the more profoundly he has studied those principles, the greater will be the good that he will derive from it. The conditions under which microscopic research has, to a large extent, to be conducted throw many difficulties in the path of the investigator, and add to the possibilities of a misinterpretation of the appearances seen. The necessity, in so many cases, of making objects translucent, and consequently the extreme thinness of the structures to be observed, destroys, to a large extent, the relation of objects to their surroundings, and leads to an imperfect conception or even a misinterpretation of the appearances. The risk, however, of such errors is now very materially diminished by recent improvements in the methods of preparing and mounting objects. One of the greatest boons which has been bestowed upon observers is the invention of that form of microtome which, by cutting serial sections, enables the observer to build up a part, and, in his mind's eye, to see it, not in one plane only, but as a solid body, and to restore its form.

The extreme delicacy also of many objects, more especially the tissues of animals and plants, throws difficulties in the way of accurate observation. But here, again, the various methods of hardening and staining have removed many of these difficulties, and have enabled us to form much more reliable conceptions of structure, and of the changes which take place in organs, during the discharge of their functions. For amongst the most remarkable and important additions to our knowledge which the microscope has enabled us to gain is the difference between the appearance of a tissue or organ when passive, or in a state of rest, as compared with its appearance when actively at work, and it is in this connection that the microscope has proved so important a boon to the physiologist. The movements of white corpuscles and other amœboid bodies, the phenomena of muscular contraction, the altered appearance of glands when engaged in active secretion, the changes which take place in cells during multiplication, are all cases in point.

As myself engaged in biological studies, it is only natural that my attention should have been more particularly directed to the use of the microscope in connection with them, and to the influence which it has exercised on their advancement. Since the time of Hooke, Grew, Malpighi, and Leeuwenhoek, this influence has been continuous and progressive. The discovery that by certain combinations of lenses an achromatic field could be obtained, enabled practical opticians to construct objectives of a magnifying power and capacity for definition far superior to any that had previously been employed. These improvements in the instrument in their turn led to discoveries of the utmost value in the structure of plants and animals, and to generalisations of a wide-reaching importance.

One of, if not the most fundamental of these discoveries, was the recognition of the anatomical unit, which we call a CELL, as a common element in the structure of organisms. Our conceptions of the structure of cells, of the relative function of their constituent parts, and the mode in which cells are developed and multiply, has varied very materially from time to time. I purpose to pass in review those aspects of the subject which have attained prominence, and have influenced the course of investigation.

It is useful occasionally to look into the history of the progress of a science, or of one of its departments; for it brings before us the difficulties which our predecessors have had to contend with in arriving at a correct conception of the inner meaning of things. It shows us how they have struggled step by step more or less accurately to interpret the facts of nature. It recalls the names of the men who have contributed to the advance of knowledge, and who in our constant striving after that which is new, are apt to be put on one side and forgotten. It enables us to see where errors in observation or in interpretation have been committed by our predecessors. If the history of Science be wisely read, it teaches us not to be too dogmatic in the promulgation of our opinions; for if the men who have gone before us have committed mistakes, rely upon it that we also cannot follow out our career without stumbling.

DR ROBERT HOOKE was one of the first men of science to employ the Microscope in the study of the structure of plants and animals. A chapter in his *Micrographia*[1] is entitled "Of the Schematisme or Texture of Cork and of the Cells and Pores of some other such frothy Bodies." This is probably the first use of the word CELL in histological description. In the course of this chapter he refers to the lightness of Cork, which he compares with froth, or an empty Honey Comb. Its substance, he says, is wholly filled with air, which "is perfectly enclosed in little Boxes or Cells distinct from one another." Further, he gives an idea of the dimensions of these cells by stating that about sixty could be placed endways in the $\frac{1}{18}$th part of an inch, and that 1,166,400 could be placed in a square inch. He thinks that they are the channels through which the juices of the plant are conveyed.

The term Cell was also employed to express a definite morphological unit by Dr Nehemiah Grew,[2] who shares with Malpighi the glory of being one of the fathers of vegetable physiology. When describing in his Anatomy of Plants the skin of the root (p. 62), he says the parenchymous material is

[1] London, 1665.
[2] *The Anatomy of Plants*, London, 2nd ed., 1682. The several Books into which Grew divided his treatise were presented to the Royal Society of London at various dates between 1671 and 1675.

"frequently constructed of exceeding little *Cells* or *Bladders*, which, in some Roots, as of Asparagus, cut traverse, and, viewed through a Microscope, are plainly visible. These Bladders are of different sizes; in Buglos larger, in Asparagus less, and sometimes they coincide and disappear."

In his account of the parenchyma of the bark he again uses the word Cells (p. 64), and says that

"each is bounded within itself, so that the *Parenchyma* of the *Barque* is much the same thing as to its Conformation, which the Froth of *Beer* or *Eggs* is as a fluid, or a piece of fine *Manchet* as a fixed body."

These cells are so small as "scarcely, without the microscope, to be discerned;" more usually, however, Grew applies to them the term bladders or vesicles. In the chapter on the vegetation of roots he speaks of the sap swelling and dilating the bladders, and as being fermented therein, as transmitted from bladder to bladder, and leaving certain of its principles adhering to them. He thus recognised that the cells or bladders played an important part in the nutrition of the plant. Almost, indeed, he seemed to have grasped the idea that they exercised a selective or secreting influence; for, in describing the parenchyma of the fruit of the lemon, he speaks (p. 180) of "those little *Cells* which contain the essential Oyl of the fruit," whilst, he says, in other bladders, "lies the acid juyce of the limon."

Malpighi, whose work on the Anatomy of Plants[1] was almost cotemporaneous with the treatise of Grew, had also seen the structures which Grew named cells or bladders, and had designated them *utriculi*, and believed that they could be separated from each other. In a subsequent treatise[2] he described the lobules of fat in animals as consisting of adipose vesicles.

Leeuwenhoek, in the course of his microscopic inquiries into the structure of plants, gave the name of *globules* to many of the objects which we now term cells, though he expressly states that they were not perfect spheres.[3]

[1] *Anatome Plantarum*, London, 1675. [2] *Opera*, vol. ii. p. 41, 1686.

[3] Samuel Hoole, who translated many of Leeuwenhoek's writings (London, 1799, part 2, p. 178), when describing fig. 11, on pl. vi., says that the globules of meal are enclosed as it were in cells, and that some of those cells are represented at H. in the figure. Leeuwenhoek himself, however, in his description of the same figure (*Epistolæ physiologicæ*, Delphis, 1719, p. 25), does not use the word cellula.

Clopton Havers, in his treatise on the skeleton, described[1] the vesicular structure of the marrow, and compared it, when seen under the microscope, to a heap of pearls.

Alex. Monro, *primus*, in his work on the bones,[2] when writing on the medullary structure, stated that it is subdivided

"into communicating vesicular Cells, in which the Marrow is contained. Hence it is that the Marrow, when hardned and viewed with a Microscope, appears like a Cluster of small Pearls. This Texture is much the same as what obtains in the other cellular parts of the Body where Fat is collected, only that the Cells containing the Marrow are smaller than those of the *Tunica adiposa* or *cellulosa* elsewhere."

Caspar F. Wolff[3] also recognised that fat was contained in small vesicles, surrounded by a fine membrane. He conceived also that the developing organs, both of plants and animals, consisted of a viscous substance which contained cavities, cells, or bladders which communicated with each other.

Fontana figured the fat vesicles, both free and surrounded by the fibres of the areolar tissue.[4]

Mirbel, in his botanical writings,[5] published at the beginning of the present century, stated that vegetables were composed largely of cells. He described *le tissu cellulaire* as composed of *les cellules*, which were contiguous with each other, so that the walls were in common. These walls were extremely thin and translucent, and sometimes riddled with pores. The term cells was also used both by his contemporaries and successors in their writings on the anatomy of plants.

But anatomists experienced much greater difficulty in distinguishing the presence of cells in the textures of animals. It is true that from the time of Malpighi and Leeuwenhoek, the globules or particles had been recognised in the blood, but it is

[1] *Osteologia nova*, 1691, p. 167.

[2] *Anatomy of the Humane Bones*, Edinburgh, 1st ed., 1726; 2nd ed., 1732.

[3] *Theoria Generationis*, editio nova, 1774; Commentary "*Ueber die Nutritionskraft*," by Blumenbach and Born, St Petersburgh, 1789.

[4] See his Essay "*Sur la structure primitive du corps animal*" in his "*Traité sur le vénin de la Vipere*," Florence, 1781 (Ph. viii. figs. 19, 20).

[5] *Traité d'Anatomie et de Physiologie végétales*, t. i., Paris, An x.; *Exposition de la Theorie de l'organisation végétale*, Paris, 1809. Ch. Robin, in the article "Cellule," *Dict. Encyclop. des Sciences médicales*, Paris, 1873, credits Mirbel with having introduced the term "cellules," but the extracts given in the text show that its English equivalent, cells, had been in use for upwards of a century before Mirbel wrote.

only within a comparatively recent period that their cellular structure was determined. Both Bichat[1] and Béclard,[2] in their important treatises on General Anatomy, made no reference to cells as elements of the tissues. Both these authors had chapters *du tissu cellulaire* or *du système cellulaire,* a term which had been in use from the early part of the last century. But by the tela cellulosa or cellular tissue, anatomists meant that form of tissue which we now more appropriately call areolar tissue; the so-called cells of which are not microscopic closed vesicles, but areolæ or spaces bounded by the fibres or laminæ of which the tissue is chiefly composed.[3] Béclard, in his description of the adipose tissue, stated that the lobules of fat consisted of microscopic vesicles $\frac{1}{100}$ to $\frac{1}{800}$ of an inch in diameter. The vesicles, he says, have walls, but they are so thin as to be indistinguishable. The presence of organised vesicles or globules in the tissues of animals had thus been recognised, but it needed further observations and facts in order to bring them into association with the cells of vegetable tissue.

This was supplied by the discovery in 1831 by the great English botanist, Robert Brown, of the "nucleus" or "areola" in the cells of the epidermis, and other tissues in Orchideæ and many other families of plants.[4] Following closely upon this discovery were the observations of Schleiden, published in 1838,[5] that the nucleus was a universal elementary organ in vegetables. Schleiden also came to the conclusion that the nucleus must hold some close relation to the development of the cell itself, and he consequently called the nucleus a "cytoblast."[6] Schleiden further discovered that the cytoblasts contained one or more minute circumscribed "spots," or "rings," or "points," which he

[1] *Anatomie générale*, Paris, 1812.

[2] *Élémens d'Anatomie générale*, Paris, 1823.

[3] The term cellular tissue was originally applied to this texture from a fancied resemblance to the proper cell tissue of plants; the walls of the cells of which were believed to be formed of a framework of fine fibres.

[4] "Organs and Mode of Fecundation in Orchideæ and Asclepiadeæ," *Trans. Linn. Soc.*, vol. xvi., 1833; reprinted in *Miscellaneous Botanical Works*, vol. i. p. 511, Ray Society edition.

[5] "Beiträge zur Phytogenesis," *Müller's Archiv*, 1838, p. 137.

[6] Fontana (*op. cit.*) figured the "globules" or scales of the epidermis, in which he recognised the nucleus, but he neither gave it a special name, nor knew its importance (plate i. figs. 8, 9, 10).

considered to be formed earlier than the cytoblasts, and which were regarded by him as hollow globules, and were subsequently named by Schwann "nucleoli."

The cellular structure of some of the animal tissues had also begun to be recognised. Turpin had noticed the resemblance between the epithelium corpuscles found in vaginal discharges and the cells of plants. Johannes Müller had discovered that the chorda dorsalis of fishes was composed of separate cells provided with distinct walls, though he did not detect a nucleus in them. Purkinje, Von Baer, Rudolph Wagner, Coste, and Wharton Jones had seen the germinal vesicle within the animal ovum. E. H. Schultz had observed the nucleus in the blood globules, and Valentin and Henle had seen it in the cells of the epidermis. The way was thus prepared for a fuller recognition of the essential correspondence between the elementary tissues of plants and animals and for a wider generalisation. Science had not long to wait for an observer who could take a comprehensive grasp of the whole subject; and in 1839 Theodore Schwann published[1] his famous researches into the structure of animals and plants, in which he announced the important generalisation that the tissues of the animal body are composed of cells, or of materials derived from cells:—

"That there is one universal principle of development for the elementary part of organisms, however different, and that this principle is the formation of cells."

Both Schleiden and Schwann entertained the idea, which had long before been present in the mind of Grew, that a cell was a microscopic bladder or vesicle. In its typical shape they regarded it as globular or ovoid, though capable of undergoing many changes of form. This vesicle possessed a cell-membrane or wall, which enclosed contents that were either fluid or somewhat more consistent. Either attached to the wall or embedded in it was the nucleus, which in its turn contained the nucleolus. Schwann, however, recognised[2] that many cells did not exhibit any appearance of a cell-membrane, but seemed to be solid, and had their external layer somewhat more compact. As showing,

[1] "Mikroskopische Untersuchungen," 1839; and Preliminary Notices in Froriep's *Notizen*, 1838.

[2] P. 176 of Sydenham Society's translation of *Schwann's Memoir*.

however, the importance which Schwann attached to the cell-wall, I should state that he regarded the chemical changes or metabolic phenomena as he termed them, as being chiefly produced by the cell-membrane, though the nucleus might participate. He explained the distinction between the character of the cell contents and the cytoblastema external to the cell, to the power exercised by the cell-membrane of chemically altering the substances, which it is either in contact with or has imbibed, and also of separating them so that certain substances appear on the inner and others on the outer surface of that membrane. In this way, he accounted for the secretion of urea by the cells lining the uriniferous tubes, and for the changes which not unfrequently take place in the cell-membrane itself by thickening or deposition of layers on or within it.

Schwann described the nucleus as either solid or hollow and vesicular, in the latter case being surrounded by a smooth structureless membrane; whilst the contents of the nucleus, other than the nucleoli, were in his view either pellucid or very minutely granulous.

Both Schleiden and Schwann conceived that in the formation of a nucleus a nucleolus was first produced, that around it new molecules were deposited for a certain distance, and then a nucleus was formed. When the nucleus had reached a certain stage of development, new molecules were deposited upon its exterior so as to form a stratum, which when thin was developed into a cell-membrane, but when thick only its outer portion became consolidated into a cell-membrane. Immediately the membrane became consolidated its expansion proceeded by the progressive reception of new molecules; the cell-wall separated from the cell nucleus, and a vesicle was formed; the intermediate space at the same time became filled with fluid, which constituted the cell contents.

Schleiden contented himself with little more than a simple statement of what he conceived to be the process of cell formation in plants; but Schwann entered into an elaborate survey of cell-life both in animals and plants, and founded on it a theory of cells applicable to all organisms.

Schwann conceived that there existed in organised bodies a solid amorphous or fluid substance to which he gave the name *cytoblastema;* this substance might be contained either within cells already existing, or else be situated in the interspaces between cells; and he believed that the cytoblastema for the lymph and blood corpuscles is the fluid lymph-plasma and liquor sanguinis in which these corpuscles float. He held that in the cytoblastema new cells are formed in the manner just described. In animals he says it is rare for cells to arise within pre-existing cells; more usually they arise in a cytoblastema external to the cells already present. Schleiden, on the other hand, maintained that in plants new cells were never formed in the intercellular substance, but only within pre-existing cells. The idea obviously present in the mind of Schwann was that the process of cell formation in a cytoblastema had some affinity with that of crystallisation. He figuratively compares the cytoblastema to a mother-liquid in which crystals are formed. He speaks of molecules being deposited around a nucleolus to form a nucleus; of a nucleus growing by a continuous deposition of new molecules between those already existing; and of the cell being formed around the nucleus by a progressive deposition of new molecules; and in more than one passage he indicated that this deposition is a precipitation. He obviously considered the principle of formation of the cell around the nucleus as the same as that of the nucleus around the nucleolus, a process which Valentin subsequently described as heterogeneous circum-position.

But Schwann at the same time showed that, with reference to the plastic phenomena, cells differed from crystals in form, structure, and mode of growth; for whilst a crystal increases only by the external apposition of new particles, a cell grows both by that method and by the intussusception of new matter between the particles already deposited. The difference, he says, is yet more marked in the metabolic phenomena, which he conceived to be quite peculiar to cells. Cells and crystals, however, he considered resembled each other in this point, that solid bodies of a definite and regular shape are formed in a fluid at the expense of a substance held in solution by that fluid, for both attract the substance dissolved in the fluid. Schwann concluded his memoir by advancing, as a possible hypothesis, the view that organisms are nothing but the form under which substances capable of imbibition crystallise; and although this hypothesis involved very much that is uncertain and paradoxical, yet he considered it to be compatible with the most important phenomena of organic life. Schwann inclined, therefore, to a physico-chemical explanation of cell-formation and cell-growth.

Shortly after the publication of Schwann's famous memoir, Henle, who had for some years been engaged in microscopic investigations on the tissues, published his well-known treatise on General Anatomy.[1] He attached great importance in cell formation to extremely minute particles, $\frac{1}{6000}$ to $\frac{1}{12000}$ of an inch in diameter, which he called *elementary granules*. He conceived that these appeared in a blastema, that several aggregated together to form a nucleus, in connection with which he thought it not improbable that a cell subsequently formed. He looked upon the elementary granules as the first and most general morphological elements of the animal-tissues, and he regarded them as vesicles consisting of excessively minute particles of oil coated with a film of albumen. It should be stated that Henle's observations on cell formation were conducted to a large extent on the products of inflammation, and on the lymph and chyle, in all of which fatty and granular particles abound.

As regards the part which the nucleus plays in the process of cell formation, both Schleiden and Schwann regarded it as of prime importance, though in the subsequent life of the cell they considered that its function terminated. Schleiden stated that, subject to certain exceptions which he enumerated, it is rare for the cytoblast to accompany the cell through its entire vital process—that it is often absorbed either in its original place, or cast off as a useless member, and dissolved in the cavity of the cell. Schwann, whilst contending for the exceedingly frequent, if not absolutely universal, presence of the nucleus, yet held that in the course of time it usually became absorbed and disappeared, so that it had no permanent influence either on the life of the cell or the reproduction of young cells, though he recognised that it remained in the blood corpuscles of some animals. Henle, again, maintained that, as there are nuclei

[1] *Allgemeine Anatomie*, Leipsic, 1841; also French translation by Jourdan in *Encyclopédie Anatomique*, vols. vi., vii., Paris, 1843.

without nucleoli, so also cells exist without nuclei, and that new cells may arise without the least trace of cytoblasts.

At about the same time, and also immediately after the publication of the important investigations by these eminent German observers, a young graduate of medicine of the University of Edinburgh, Dr Martin Barry, stimulated, he says, by the researches and encouraged by the friendship of Johannes Müller, Ehrenberg, Rudolph Wagner, and Schwann, undertook elaborate researches into the structure of the ovum, more especially in mammals. His results were published in a series of memoirs printed in the *Transactions of the Royal Society of London* from 1838 to 1841.[1] In these embryological memoirs, Barry announced several important discoveries. In his first memoir (1838) he pointed out that the germinal vesicle which had been discovered in the mammalian ovum by M. Coste and Mr Wharton Jones, was the first part of the ovum to be formed both in mammals and birds, and he thought that this was probably the case throughout the animal kingdom. In his second memoir (1839) he extended to the mammalian ovum an observation which had been made by Prevost and Dumas on the ovum of the frog, and by Rusconi on the ovum in osseous fish. He described the formation within the rabbit's ovum of the body which he named, and which has been known since his time as the mulberry-like structure. This body arose at first as two vesicles, then as four, and so on in multiple progression, so that Barry was the first to recognise in the ovum of mammals the process which we now know as the segmentation of the yelk. He showed that the vesicles of the mulberry body were cells, and that each contained a pellucid nucleus, and that each nucleus presented a nucleolus. Further, these vesicles arranged themselves as a layer within the zona pellucida.

Barry's third memoir was published in 1840, and as he gave it the subsidiary title of "A Contribution to the Physiology of Cells," it is clear that he regarded his embryological inquiries

[1] *Phil. Trans.*, vols. cxxviii.–cxxxi. The value which was attached to these Memoirs at the time may be estimated by the fact that the Royal Society of London awarded to their author in 1839 one of the Royal Medals. The neglect into which Dr Barry's writings have fallen is largely due to the disbelief in his subsequent descriptions of the spiral structure of muscular fibre, of blood-corpuscles, and indeed of the elements of the tissues generally.

as having an important bearing on the facts of cell-formation and function. He repeated his observations on the formation of the mulberry-like body, and now recognised that its component cells had been derived from the germinal vesicle, the contents of which entered at first into the formation of two cells, each of which presented a nucleus which resolved itself into other cells, and by a repetition of this process, the cells within the ovum became greatly augmented in number. Further, he stated that the whole embryo at a subsequent period is composed of cells, filled with the foundations of other cells. Although we may not agree with all the details given by Barry in his account of these observations, yet there can be no doubt that he had early recognised the important fact, that in animals new cells arose within pre-existing cells, as Schleiden had affirmed to be the case in plants, and that the nucleus acted as an important centre for the production of young cells. In recognising the endogenous reproduction of young cells in animals, Barry made an important advance on the view entertained by Schwann, who regarded the endogenous production of cells as quite exceptional amongst animals.

In this same memoir Barry incidentally mentioned that he saw in the ovum of the rabbit a cleft or orifice in the zona pellucida, and that on one occasion he observed what he believed to be the head of a spermatozoon within the orifice. Two years afterwards he read to the Royal Society[1] a short paper, in which he announced that he had seen a number of spermatozoa within the ova of the rabbit, and in October 1843 he published a figure of an ovum with spermatozoa in its interior.[2]

In a memoir on the Corpuscles of the Blood, published in 1841, Barry announced a still more definite conception of the function of the nucleus. He directly traversed the statement of Schleiden, that the nucleus, after having given origin to the cell-membrane, has performed its chief office, and is usually cast off and absorbed; as well as that of Schwann, who had never, except in some instances in fat cells, observed anything to be produced by the nucleus of the cell. Barry stated that the nucleus is a centre for the origin,

[1] *Phil. Trans.*, vol. cxxxiii.; read Dec. 8, 1842.
[2] "On Fissiparous Generation," *Edin. New Phil. Jour.*, Oct. 1843.

"not only of the transitory contents of its own cell, but also of the two or three principal and last formed cells destined to succeed that cell; and in fact, that by far the greater portion of the nucleus, instead of existing anterior to the formation of the cell, arises within the cavity." Further, he says, "young cells originate through division of the nucleus of the parent cell, instead of arising as a sort of product of crystallisation in the fluid cytoblastema of the parent cell."

He regarded the division of the nucleus in pus corpuscles as not artificially produced by the agency of acetic acid, as was held by Henle and Schwann, but as a part of the process by which cells were produced, and apparently universal in its operation.

In a paper published in 1847, Dr Barry summarised his observations on the nucleus of animal and vegetable cells, and whilst expressing certain opinions on the mode of formation of the nucleolus and nucleus and the growth of cells which cannot now be accepted, he continued to maintain that cells are descended from an original mother cell by cleavage of the nucleus, and all subsequent nuclei are propagated in the same way by fissiparous generation. Every nucleus, therefore, was a sort of centre, inheriting more or less the properties of the original nucleus of the fecundated ovum, which he conceived to be the germinal spot, and exercising an assimilative power. Dr Barry's contributions to a correct conception of the development of cells, are of the highest importance when viewed in the light of modern observations.

But another Edinburgh inquirer, Mr John Goodsir, afterwards as Professor Goodsir, the distinguished occupant of the chair of Anatomy in the University of Edinburgh, was engaged between the years 1842 and 1845 in studying the processes of cell-life, both in healthy tissues and in certain pathological conditions.[1] In his important memoir on Secreting Structures, published in 1842, he demonstrated from a variety of examples that secretion is a function of the nucleated cell, and he gave, as one of his many illustrations, the cells of the testis contain-

[1] "On Secreting Structures," *Trans. Roy. Soc. Edin.*, 1842; "On Peyer's Glands," *London and Edinburgh Monthly Journal*, April 1842; "On Structure of Human Kidney," *ibid.*, May 1842; *Anatomical and Pathological Observations*, Edinburgh, 1845; also, his collected papers in *Anatomical Memoirs*, Edinburgh, 1868, edited by W. Turner.

ing spermatozoa which were derived from the nuclei of these cells. In the original memoir he was inclined to believe that the cell wall was the structure engaged in forming the secretion; but in a reprint of it in 1845, he modified that view, and gave as his opinion that the secretion would appear to be a product of the nucleus. Goodsir also stated in the memoir of 1842 "that the nucleus is the reproductive organ of the cell, that it is from it, as from a germinal spot, that new cells are formed," and he cited cases in which it became developed into young cells. He subsequently, in a short paper on Centres of Nutrition, extended this view to the tissues generally. He defined the nutritive centres as minute cellular parts, existing, for a certain period at least, in all the tissues and organs. They drew from the capillary vessels or other sources nutritive material, which they distributed to the tissues and organs to which they belonged. He regarded a nutritive centre as a cell, the nucleus of which is the permanent source of successive broods of young cells, which from time to time fill the cavity of their parent. He called this central or capital cell the mother of all those within its own territory or department. Goodsir also showed that cells were important agents in Absorption, Ulceration, and Inflammation. In inflammation of cartilage, for example, he described and figured the cells in the area affected as increased in size, modified in shape, and crowded with a mass of nucleated cells in their interior, through the agency of which the walls of the corpuscles and the hyaline matrix became absorbed. He also gave illustrations of the multiplication of nuclei within cells in the course of formation of cysts. Corroborative observations on endogenous formation within animal cells were also given by Mr H. D. S. Goodsir, as confirmatory of the doctrine propounded by his brother on the cell as a centre of nutrition, secretion, and production of young cells. In a research into the structure of the testis in Decapodous Crustacea, Henry Goodsir observed that the head of the spermatozoon corresponded with the nucleus.

The conception entertained both by Martin Barry and John Goodsir of the process of cell-formation and of the function of the nucleus was in the main very different from that propounded by Schleiden and Schwann. Whilst agreeing with

Schleiden in holding that new cells were formed within parent cells, they did not look upon the process as one of deposition, in the first instance around a nucleolus and then around a nucleus, but they regarded the nucleus as the prime factor by the division of which new cells were formed. With regard to the free formation of cells, as it was not unfrequently called, by deposition in a cytoblastema situated external to existing cells, to which Schwann and Henle attached so much importance in animals, they gave no concurrence. Both Barry and John Goodsir had grasped and advocated the fundamental principle, both of the endogenous development of cells from a parent centre and of an organic continuity between a mother cell and its descendants through the nucleus; and the brothers Goodsir had applied this principle in their anatomical, pathological, and zoological researches.

As regards the physiological action of cells, Mr (now Sir William) Bowman had expressed the opinion[1] that there was a strong presumption that the epithelium of glands assimilated the secretion from the blood. That the secretion might be separated, either by the passage of its elements through the cells; or by the cells undergoing solution or deliquescence; or by the cells being cast off entire with their contents. Mr (now Sir John) Simon also expressed, in 1845, some important general conclusions on the physiological action of cells.[2] He looked upon the cell wall as of secondary importance and of inessential formation, and he regarded the nucleus with the material developed around it as constituting the sole physical evidence of activity in the part. He saw bile and other secretions within cells, and stated that when the products of secretion can be seen within a cell, they are accumulated in the portion which corresponds to the nucleus as though it were the true centre of attraction. Simon also observed the development of spermatozoa within cells, and had seen one end adhering to the relique of a cell, probably its nucleus.

Histologists elsewhere had made isolated observations on the development in the animal body of young cells within

[1] Article "Mucous Membrane," in Todd's *Cyclopædia*, date probably 1842 or 1843.

[2] *Essay on the Thymus Gland*, London, 1845.

parent cells. Even before the publication of Schwann's immortal treatise, Turpin had stated that the corpuscles which he found in vaginal discharges contained a new generation in their interior, and Dumortier had described secondary cells as formed in the ova of snails. These observations exercised, however, no influence on the progress of thought; and Schwann, though referring to them in the preface to his treatise, yet appeared to question their accuracy.

In 1841, Robert Remak published[1] an account of what he saw in the blood corpuscles of the chick, some of which were biscuit-shaped. At each end was a nucleus, and the two nuclei were connected together by a thin stalk which traversed the intermediate part of the corpuscle. He thought it probable from these observations that a multiplication of blood corpuscles through division occurred. He obtained also similar evidence in the blood of the embryo pig, and saw both in the blood of the horse and of man red blood-cells formed in the interior of large mother cells. It is customary in Germany to credit Remak with being the first to recognise the division of the nucleus within the cell as a stage antecedent to, and associated with, the division of the cell itself; but from what has already been stated, it will be seen that Martin Barry had preceded him by some months[2] in the recognition of the importance of division of the nucleus in the production of young cells.

In 1843, Albert von Kölliker published[3] an interesting memoir on the changes which take place in the fertilised ova of various

[1] *Medicinische Zeitung*, p. 127, July 7, 1841.

[2] Barry's later memoirs were read to the Royal Society of London, May 7, 1840; January 7, 1841; June 17 and 23, 1841. They are illustrated with numerous beautiful figures, in which the division of the nucleus and the endogenous production of young cells are shown. Further, it should be kept in mind that Remak's observation was on a single tissue, the embryonic blood corpuscle; whilst Barry's was a generalisation based on a large series of researches on the ovum, blood and mucous corpuscles, epithelium and other cells. John Goodsir, in a footnote to his important paper "On Centres of Nutrition," already referred to in text, p. 18, says—"For the first consistent account of the development of cells from a parent centre, and more especially of the appearance of new centres within the original sphere, we are indebted to the researches of Dr Martin Barry." Remak subsequently extended his observations, on the multiplication of cells through division of the nuclei, to the ovum, and the cells of the tissues generally. See *Müller's Archiv*, 1852, p. 47, and *Untersuchungen über die Entwicklung der Wirbelthiere*, 1855.

[3] *Müller's Archiv*, 1843.

parasitic worms. He described and figured the production in regular progression of young cells within the ovum, and observed that in some cells the nucleus was elongated; in others constricted in the middle, as if about to divide; in others two nuclei were present, each smaller than the single nucleus of adjoining cells, as if they had arisen from the division of a larger nucleus. A legitimate inference from these observations was that in the formation of young cells, the nucleus of the parent cell divided into two, and that each of these gave origin to a new cell.

The endogenous multiplication of animal cells by division of the nucleus now began to be more widely recognised. It was described by Kölliker and by Mr (now Sir James) Paget in the blood corpuscles of the embryo, by Kölliker in cartilage and in the giant cells of the marrow of bones, and by various observers in the fertilised ovum. It acquired, therefore, much more importance as a mode of origin of animal cells than was accorded to it by Schwann.

At the time when I began the study of anatomy and physiology in 1850, the current teaching of the schools embraced two methods of cell formation,—the one through the intermediation of existing cells, which might be either by endogenous production within a mother cell through division of the nucleus, or by fissiparous division, or by budding off of a part of a cell; the other by a process of free cell-formation outside existing cells and within a blastema. When I came to Edinburgh in 1854 to act as Demonstrator of Anatomy, I found that the biologists were divided into two hostile forces,—the one was presided over by Professor John Goodsir, whose views on the intracellular origin of new cells I have already explained, and which he systematically expounded in his lectures; the other was led by the then Professor of the Institutes of Medicine, Dr Hughes Bennett. Dr Bennett, whose investigations into cell-formation and cell-life had been largely based, like those of Henle, on the study of pathological processes, was led to attach great importance to the granules or molecules which abound in the so-called inflammatory exudations and in purulent fluids. Bennett held that molecules arose in an organic fluid, and that an aggregation of molecules produced nuclei, upon which cell walls may be formed; that the molecule was the primary, elementary and most simple form of organised matter, and that an aggregation of molecules might even form fibres and membranes without the agency of cells. His views were almost a reproduction of those of Henle, and he advocated them with great vigour and persistency, especially in regard to the production of pus and other products of inflammation.

Pathologists had indeed very generally supported the theory of the free formation of cells in exudations; but this view, however, was not universally entertained by them. Professor Goodsir[1] and Dr Redfern[2] had shown its inapplicability in inflammation and ulceration of articular cartilages. Professor Virchow, in a series of papers in his *Archiv*, commencing with vol. i. in 1847, had described the endogenous formation of young cells in pathological structures. In his lectures on Cellular Pathology, published in 1858, Virchow, like Goodsir, announced his belief in the mapping out of the body into cell territories. Virchow's conception of the territory was the intercellular substance immediately surrounding a cell, and subject to its influence.[3] He maintained that in pathological structures there was no instance of development *de novo*, but that where a cell existed, there one must have been before. He called it the law of continuous development, which could be formulated in the expression *omnis cellula e cellula*. He adduced a great variety of specific instances to show the diffusion throughout the tissues and organs of nucleated cells, and he established, by a variety of proofs, the important part played by the cell elements, more especially those of the connective tissue, in the inflammatory process and in the production of new formations. He advanced, indeed, such a mass of evidence in support of this position, that the theory of free cell formation was shortly after abandoned in connection with pathological processes, as it had been some time previously by most observers in normal histiogenesis.[4]

[1] *Op. cit.*, 1845.

[2] "Abnormal Nutrition in Articular Cartilages," *Edinburgh Monthly Medical Journal*, August 1849; and separate *Memoir*, Edinburgh, 1850.

[3] He first used the term Zellen Territorien in his *Archiv*, Bd. iv., 1852, p. 383.

[4] In a Lecture which I delivered before the Royal College of Surgeons, Edinburgh, in 1863 (*Edinburgh Medical Journal*, April 1863), I summarised the evidence of the derivation of pathological cell formations from pre-existing cells, and adduced additional examples from my own observations.

The continued investigations into the structure of cells, both in plants and animals, led to modifications in the conception of their morphology. Hugo von Mohl announced that he had discovered[1] in the vegetable cell, after being acted on by alcohol and iodine, a thin nitrogenous membrane distinct from and applied to the inner surface of the cellulose wall of the cell, which he named the *primordial utricle*. He regarded it as forming a vesicle within the cell wall, and containing the contents and the nucleus. By subsequent observers it has been shown that the primordial utricle is nothing more than a thin layer of protoplasm lying close to the cellulose wall, and enclosing the sap cavity of the cell.

Professor Huxley, in an article on the Cell Theory,[2] criticised the views of Schleiden and Schwann, and introduced the terms *endoplast* and *periplast* into histological description. He regarded the primordial utricle as the essential part of the endoplast in the plant, and as homologous with the "nucleus" of the animal cell; whilst the protoplasm and nucleus were simply its subordinate modifications. The periplast, on the other hand, consisted in plants of the cellulose cell wall; whilst in animals the cell wall and matrix of cartilage, the cell walls and intercellular substance of connective tissue, the calcified matrix of bone, and the sarcous elements of muscular fibre were all examples of periplast which had passed through various forms of chemical and morphological differentiation. Huxley maintained that the periplast was the metamorphic element of the tissues, and by its differentiation every variety of tissue was produced, owing to intimate molecular changes in its own substance. The endoplast again might grow and divide, as in the process of cell multiplication; but it frequently disappeared and underwent neither chemical nor morphological metamorphosis; and so far from being a centre of vital activity, he held that it exercised no attractive, metamorphic, or metabolic force upon the periplast.

But about this time it began to be more distinctly recognised that many anatomical units which were to be regarded

[1] *Botanische Zeitung*, translated by A. Henfrey in Taylor's *Scientific Memoirs*, vol. iv., 1846.

[2] *British and Foreign Medico-Chirurgical Review*, Oct. 1853.

as cells, as Schwann had indeed admitted in a few exceptional cases, possessed no cell wall or investing membrane, and that the analogy with a bladder or vesicle could no longer be sustained. Thus in 1856,[1] Leydig gave as his idea of a cell a more or less soft substance, approaching in its original state to the globular in form, which enclosed a central body, the nucleus. Subsequently, the cell substance might harden into a more or less independent membrane, and the cell would then consist of membrane, contents, and nucleus. Leydig's conception therefore of what were the essential parts of a cell closely corresponded with the opinion expressed some years previously by John Simon. Brücke again maintained[2] that the constancy of the presence of a nucleus was subject to certain limitations, especially in the cells of cryptogams, and that there was no positive information either respecting the origin or the function of the nucleus. He further showed that the soft contents of the cell were of a highly complicated nature, and that they frequently exhibited spontaneous movements and contractility. In 1861 and also in 1863, Max Schultze published[3] most important papers on the properties of cells. He adopted the term protoplasm which Von Mohl had employed to designate the contents in vegetable cells which surround the nucleus, and applied it to the substance which had the corresponding position in animal cells. He completely discarded the view that a membrane was essential to a cell, and defined a cell as a nucleated mass of protoplasm. He identified the protoplasm of the animal and vegetable cell as essentially the same substance as the contractile sarcode which forms the freely moving pseudopodia of the Rhizopoda, and he looked upon it as possessing great physiological activity. The conception of the functions and relative importance of the constituent parts of a cell had now undergone a material change. The suggestive ideas of Simon and Leydig had been distinctly formulated by Max Schultze. Instead of the cell membrane being regarded as a necessary part of a cell, and the active element concerned in the formation of the cell contents, as Schwann

[1] *Lehrbuch der Histologie*, 1857. Preface dated October 1856.
[2] "Elementarorganismen," *Wien Sitzbericht*, 1861.
[3] *Müller's Archiv*, 1861, p. 1; *Das Protoplasma*, Leipzig, 1863.

believed, it now became universally recognised as only a secondary structure formed by a differentiation of the superficial part of the protoplasm. Schultze also maintained that the appearance of the membrane might be looked upon as a sign of commencing loss of activity, for a cell with a membrane can no longer divide as a whole, but the division is restricted to the protoplasm contained within it. A cell with a membrane is, he says, like an encysted Infusorian. Taking the embryonal cell as a type, he believed that both the nucleus and the protoplasm were derived from the corresponding constituents of another cell. The protoplasm was the substance especially endowed with living force; the nucleus, he thought, played an important rôle, though its exact function could not be defined. The only structural character which Schultze recognised in the protoplasm, was a finely granular appearance throughout the somewhat jelly-like, contractile material in which the granules were embedded. Although the name of protoplasm was now given to this substance, yet it obviously corresponded morphologically with the blastema which both Schleiden and Schwann had recognised within the cell, between the nucleus and the cell wall; though it now assumed in the minds of observers a different physiological import.

The reign of protoplasm had now been inaugurated. Not only was the cell membrane believed to be a product of its differentiation, but the matrix of cartilage and of connective tissues, and the other intercellular substances, were thought to be produced not as a secretion, but by a conversion of the protoplasm of the cells into their respective forms. But, further, Max Schultze[1] described a non-nucleated Amœba; and Haeckel[2] and Cienkowski[3] other non-nucleated organisms, simple in their structure. These organisms were believed to consist solely of a clump of soft protoplasm, which might either be naked, when they were called *simple cytodes;* or encased in a wall or envelope, and then termed *encased cytodes.* Haeckel named these—the most simple of all organisms—Monera, and referred them to a group on the confines of both the animal and the vegetable

[1] *Organis. de Polythal.*, 1854.
[2] *Zeitsch. f. wiss. Zool.*, 1865, Bd. xv.
[3] Max Schultze, *Archiv*, 1865.

kingdoms, which he termed Protistæ. Stricker[1] also excluded the nucleus as necessary to our conception of an elementary organism. He went so far as to say that the historic name of cell might be applied to the morphological elements of the higher animals, or to independent living organisms, even if they were only little masses of animal sarcode or protoplasm. He was not, however, disposed to extend the definition to isolated fragments of living protoplasm, unless the whole group of phenomena characteristic of an independent organism could be recognised. Stricker held that protoplasm may be fluid, solid, or gelatinous. It exhibited the phenomena of movement, of nutrition, of growth, and the capability of reproducing its like, *i.e.*, the sum of the phenomena which are characteristic of living organisms.

The doctrine that a nucleated mass of protoplasm was the structural unit common to organisms generally, both plants and animals—though at the very bottom of the scale the phenomena of life could be manifested by a particle of protoplasm without a nucleus—received its most popular expression in this country at least, in a well-known Address by Professor Huxley.[2] In this address he stated that protoplasm, simple or nucleated, is the formal basis of all life, and that all living forms are fundamentally of one character. His views, therefore, had undergone some modification, as to the element of the tissue in which vital activity was more especially centred, since the publication of his previous article on the Cell Theory.

But contemporaneous with these researches on the protoplasmic theory of cell structure and activity, an English physiologist, Dr Lionel Beale, was conducting investigations into the structure of the simple tissues from an independent and somewhat different point of view. He considered that the elementary tissues of every living being consisted of matter in two states,[3]—the one an active, living, growing substance, composed of spherical particles, capable of multiplying itself,

[1] "Allgemeines über die Zelle," in *Handbuch der Lehre von den Geweben*, Leipzig, 1871.

[2] "On the Physical Basis of Life," a Lay Sermon delivered Nov. 8, 1868; *Fortnightly Review*, and Lay Sermons and Addresses, London, 1870.

[3] *Structure of the Simple Tissues*, London, 1861.

and coloured red by carmine, which he named *germinal matter;* the other, named by him *formed material,* was situated peripherally to the germinal matter from which it was produced; it was passive, non-living or dead, incapable of multiplying itself, and not coloured red by carmine like the germinal matter. In adapting these terms to the ordinary nomenclature of the cell, Dr Beale states—

In some cases the germinal matter corresponds to the "nucleus"; in others to the "nucleus and cell contents"; in others to the matter lying between the "cell wall," and certain of the "cell contents": while the formed material in some cases corresponds exactly to the "cell wall" only; in others to the "cell wall and part of the cell contents"; in others, to the "intercellular substance"; and in other instances to the fluid or viscid material which separates the several "cells, nuclei, or corpuscles" from each other.

According to this theory of the tissues, all the elementary parts of the body consist of two substances—an active, living, germinal matter, and an inactive, non-living, formed material. Every living elementary part is derived from a pre-existing living elementary particle. The nuclei of the germinal matter, though remaining for a long time perhaps in a comparatively quiescent state, may become active and give rise to new nuclei. Dr Beale held that the cell wall was by no means constantly present in cells, and that when present, both it and the intercellular substance were formed or produced by, or a conversion of the germinal matter. In a subsequent work, Beale[1] substituted the term *bioplasm* for germinal matter, and included in it the nucleus, nucleolus, and some forms of protoplasm. It is, he says, from the bioplasm that the formed material is produced.

An important advance was made in the conception of the structure of the constituent parts of the cell when it was ascertained that protoplasm was not the structureless, granulated jelly, or slime, which it was originally supposed to be, but that it consisted of two parts, viz., a minute network of very delicate fibrils and an apparently homogeneous substance which occupied the interstices of the network. Stilling and Max Schultze recognised the fibrillated character of the protoplasm of nerve

[1] *Bioplasm,* London, 1872.

cells and axial cylinders, but Frommann, Heitzmann, Klein, and other histologists applied the observations to the structure of protoplasm generally.

The subject made a yet greater step forwards when it was ascertained by Strasburger and Flemming that the nucleus in its passive or resting stage consists, in addition to the nucleolus, of threads or fibres, some finer, others coarser, formed of *nuclein*, and arranged in a reticular network, so as to form little knots at the points of intersection of the fibres. In the interstices of the network an apparently structureless intermediate substance, nuclear fluid or *nucleoplasm*, is situated; and the nucleus is surrounded by a membrane.[1] By some observers the threads are regarded not as forming a network, but as a greatly coiled single thread. From the affinity which they have for colouring matter so that they easily stain with dye, Flemming has named them *chromatin fibres*.[2] But the whole question of the relation of the nucleus to the life of the cell, more especially in connection with the production of young cells, assumed a much more definite form when it was discovered that the chromatin nuclear fibres took a primary part in the division of the nucleus in the process of cell multiplication. The nucleus was now reinstated in its place as of primary importance in the structure of cells, and as an essential factor in the formation of new cells. The movements of the fibres within the nucleus, and their rearrangement so as to form definite figures, which changes precede the act of division, were named by Schleicher *karyokinesis*, or nuclear movement, a term which has now been generally adopted.[3]

Waldeyer states that Schneider of Breslau was the first to recognise these movements of the nuclear fibres, and to describe them in connection with the division of the ova, the sperm cells, and also the tissue cells of a flat worm, *Mesostomum;* but

[1] This membrane is perhaps nothing more than a somewhat differentiated layer of the protoplasm of the cell arranged around the nucleus.

[2] The chromatin fibres appear to be composed of granules or spherules, named "microsome-discs" by Strasburger.

[3] Flemming proposed the term *Karyomitosis*, or nuclear threads, to express the thread-like figures formed in the process. M. Carnoy gives the name *enchylema* to the apparently structureless material which occupies the interstices of the network both of the nucleus and cell protoplasm.

Bütschli and Fol made the process more generally known. The publication of their researches excited the greatest interest, and a host of observers, amongst whom I may especially name Strasburger, Flemming, Hertwig, Balbiani, E. van Beneden, Johow, Heuser, Pfitzner, J. M. Macfarlane, Carnoy, and Rabl, demonstrated the process in a number of plants and animals, and the literature of the subject is now very extensive. In order to express the appearances presented, and the changes which take place both in the nucleus and in the cell in the process of division, a new nomenclature has been introduced, and we now read of cytaster, monaster, dyaster, equatorial plate and crown, pithode or cask-shaped, spindles, ellipsoids, coils, skeins both compact and loose, pole radiations, spirem, and other terms. From the range of the literature it would be a work of considerable labour and time to make an analysis of the different observations so as to associate with the name of each observer the particular set of facts or opinions which he has made known. Fortunately, this is unnecessary on my part, as admirable resumés of the whole subject have recently been published both by Professor M'Kendrick of Glasgow[1] and Professor Waldeyer of Berlin.[2]

Without entering into a detailed description, it may suffice my present purpose to say that four stages may be recognised in connection with nuclear division.

The *first*, or *spirem stage*, exhibits several phases. At its commencement the finer threads, which connect the primary or coarser chromatin fibres of the resting nucleus together, and which give the network-like character, have disappeared along with the knots at their points of intersection and the nucleoli. The primary chromatin fibres, or *chromosome* as Waldeyer calls them, form a complex coil, the spirem or ball of thread, which divides into loops, about twenty in number, and forms a compact skein. The loops are placed with their apices around a clear space called by Rabl the "polar field," whilst their free ends reach the opposite surface of the nucleus or the "antipole." The nucleus also increases in size cotemporaneously. The loops next become not so tightly coiled, and form the loose skein, though the individual fibres thicken and shorten. A most important

[1] *Proc. Phil. Soc.*, vol. xix., Glasgow, 1888.
[2] *Archiv für Mikros. Anat.*, Bd. xxxii., 1888.

change then occurs, which was discovered by Flemming, and which consists in a longitudinal splitting of each loop or primary chromatin fibre into two daughter threads. A spindle-shaped figure, first seen by Kowalevsky, next appears in the nucleus; it consists of threads that stain much more feebly than the chromatin fibres.[1] The spindle has two poles and an equator, and it finally occupies a position in the deeper part of the nucleus; its equator lies in the plane, through which division of the nucleus is about to occur. The loops of chromatin fibres group themselves in a ring-like manner around the equator of the spindle with their angles inwards, whilst from each pole of the spindle a radiated appearance (*cytaster*) extends into the protoplasm of the cell. The membrane of the nucleus has now disappeared, so that it is directly invested by the protoplasm of the cell; and it is possible, as Strasburger thinks, that there may be a direct flow of the protoplasm into the nucleus, and that the spindle may be produced by it. At the pole of the spindle, from the point at which the cytaster radiates, E. van Beneden has seen a small, shining, polar body, which Strasburger says is not found in vegetable cells.

The *second*, or *monaster stage*. When the chromatin loops have arranged themselves about the equatorial plane of the spindle with their limbs pointing outwards, and the angle of the loop towards the centre of the spindle, a single star-like figure (*monaster*, *equatorial plate* or *crown*) is produced. The two daughter threads into which each primary chromatin thread had previously split longitudinally, now separate from each other, and, according to Van Beneden and Heuser, pass to opposite poles of the nuclear spindle, where they form loops. These changes are known as the process of *metakinesis*.

In the *third*, or *dyaster stage*, the chromatin loops at each pole of the spindle arrange themselves so that the angles of the loops, though not touching each other, are close together at the pole, and the limbs of the loops are bent towards the equator of the spindle. Two stars are thus produced (*dyaster*), one at each pole, and each star is formed of one of the daughter threads into which each chromatin fibre of the monaster divides

[1] Owing to the feeble staining of the spindle figure and of the nucleoplasm, the substances which compose them have been named *Achromatin*.

by its longitudinal splitting. Each star is sometimes called a daughter skein; around each daughter skein a membrane appears at this stage, and a daughter nucleus is then formed.

In the *fourth*, or *dispirem stage*, the chromatin threads thicken and shorten, and the loops of each star arrange themselves with the angles towards the polar field of the nucleus, and the limbs to the antipole.

The division of the mother cell into two new daughter cells is now completed by the cell protoplasm gradually constricting in the equatorial plane until at last it is cleft in twain, and each daughter nucleus is invested by its own mass of protoplasm. The chromatin threads of the daughter skein then form a network of coarser and finer fibres, a nucleolus appears, and the resting nucleus of the daughter cell is completed. Two daughter cells have thus arisen, each of which possesses its own independent vitality. Owing to the very remarkable longitudinal splitting of the fibres of the chromosome, and the distribution of the daughter threads from each fibre to the opposite poles of the spindle, it follows that each daughter nucleus contains about one-half of each chromatin fibre, so that whatever be the properties of the chromosome of the mother cell, they are distributed almost equally between the nuclei of the two daughter cells. As regards the cleavage of the protoplasm, there is no evidence that such a rearrangement of its constituent parts takes place as to give to each daughter cell one-half of the protoplasm from each pole of the mother cell. It is probable that each daughter nucleus simply becomes invested by that portion of protoplasm which lies in proximity to it at the time when the constriction of the protoplasm begins. The young daughter cell, seeing that it is composed both in its nucleus and protoplasm of a portion of each of these constituent parts of the mother cell, possesses therefore properties derived from them both.[1]

Owing to the disappearance of the nuclear membrane at the end

[1] Dr J. M. Macfarlane has described as constantly present within the nucleolus of vegetable cells a minute body, which he terms *nucleolo-nucleus* or *endonucleolus*. He considers it as well as the nucleolus to become constricted and divided before the nucleus and the cell pass from the resting into the active phase of cell multiplication. See *Trans. Bot. Soc. Edin.*, 1880, vol. xiv., and *Trans. Roy. Soc. Edin.*, 1881–82, vol. xxx.

of the spirem stage of karyokinesis, at least in cells generally (though it is said to persist in the Protozoa during the whole process of karyokinesis), it follows that the nucleoplasma and the cell protoplasm cease for a time to be separated from each other, and an interchange of material may take place between them in opposite directions—both from the protoplasm to the nucleus, as Strasburger contends, and from the nucleus to the protoplasm, as has in addition been urged by M. Carnoy. In every case it should be remembered that the nucleus, being surrounded by protoplasm, can only obtain its nutrition through the intermediation of that substance, and thus there is always a possibility of the protoplasm acting on the nucleus, and in so far modifying it.

Having now sketched the progress of knowledge of the structure of cells and their mode of production, I may, in the next instance, state the present position of the subject. We have seen that the original conception of a cell was a minute, microscopic box, chamber, bladder, or vesicle, with a definite wall, and with more or less fluid contents. This conception was primarily based upon the study of the structure of vegetable tissue; and, as regards that tissue, it holds good to a large extent to the present day. For the cellulose walls of the cells of plants, with their various modifications in thickness, markings, and chemical composition, constitute the most obvious structures to be seen in the microscopic examination of vegetable tissue. Within these chambers is situated the active, moving protoplasm of the cell, and embedded in it is the nucleus; it also contains the sap, crystals, starch granules, or other secondary products. The cell wall is to all appearance produced by a conversion of, or secretion from, the protoplasm. But even in plants a cell wall is not of necessity always present; for, in the development of the daughter cells within a pollen mother cell, there is a stage in which the daughter cell consists only of a nucleated mass of protoplasm, prior to the formation of a cell wall around it by the differentiation of the peripheral part of its protoplasm. Again, the so-called non-cellular plants or Myxomycetes, before they develop their spores,[1] consist of masses of naked protoplasm, on the exterior of which, in the course of time, a

[1] *Lectures on the Physiology of Plants*, by Julius von Sachs. Translated by H. Marshall Ward, Oxford, 1887.

membrane or cell wall is differentiated; in the substance of these masses of protoplasm numerous nuclei are situated.[1]

In animal tissues the fat cell possesses a characteristic vesicular form, with a definite cell wall, but neither in it nor in the vegetable cells does the cell wall exercise any influence on the secretion either of cell contents or of matters that are to be excreted. In animal cells a cell wall is frequently either non-existent, or doubtful, and when present is a membrane of extreme thinness. Animal cells, therefore, do not have as a rule the chamber-like form or vesicular character of vegetable cells.

The other constituents of the cell, and the only essential constituents, are the nucleus and the material immediately surrounding it in which the nucleus is imbedded. It is of secondary importance whether this material be called protoplasm, or bioplasm, or germinal matter. The term protoplasm, however, is that which has received most acceptance. In adopting this term, it should be employed in a definite sense to express the translucent, viscid, or slimy material, dimly granular under the lower powers, minutely fibrillated under the highest powers of the microscope, which moves by contracting and expanding, and which possesses a highly complex chemical constitution. The term ought not to embrace either the cell wall of the vegetable or animal cell, or the intercellular substance of the animal tissues. For although these have in all probability been originally derived from the protoplasm, by a chemical and morphological differentiation of its substance, or a secretion from it, they have assumed formal and special characters and have acquired distinct functions. Protoplasm, as above defined, is a living substance endowed with great functional activity. It possesses a power of assimilation, and can extract from the appropriate pabulum the material that is necessary for nutrition, secretion, and growth. Growth takes place not by mere accretion of particles on the surface, but by an interstitial appropriation of new matter within its most minute organised particles. In cases, also, where the media in which the cell lives are suitable, as in the freely moving Amœba, or the white blood corpuscles, portions of the proto-

[1] The opinion for long entertained that the simpler algæ and fungi and cryptogams generally are destitute of nuclei has been shown by Schmidt and others to be incorrect.

plasm may separate by budding from the general mass of the cell, and assume an independent existence; but the conditions under which the budding off of protoplasm can take place are exceptional in the higher organisms. Protoplasm, therefore, according to this definition, in addition to being a moving contractile substance, is the nutritive and secreting structural element of the tissues, and is always found relatively abundant where growth and the nutritive processes are most active.

In the fertilised ovum, after the process of segmentation has begun, and in the earlier stages of development of the embryo, the cells are nucleated masses of protoplasm, without cell walls, and with no intercellular material. In the course of time, in animals more especially, an intercellular substance arises apparently by a differentiation of, or secretion from the protoplasm. In many of the tissues this substance acquires such characters, magnitude, and importance as to overshadow the nucleated masses of protoplasm which it lies between and surrounds. The intercellular substance is the principal representative of the "formed material" of Dr Beale. I cannot, however, agree with him in regarding it as passive and non-living or dead; for morphological and functional changes take place in it long after its original formation. Thus the hyaline matrix, or intercellular substance, of the young costal cartilages becomes converted into a fibrous matrix in the later period of life, and the striated substance of muscular fibre is one of the most physiologically active tissues in the animal body. In the general economy of the tissues, in the fitting of each to discharge the function for which it is specially intended, the intercellular substance plays an essential part. It gives strength to the bones, toughness and elasticity to ligaments and cartilage, motor power to muscles. It wastes by use and needs repair. But it is probably to the nucleated protoplasm within its substance that we are to look for the structural element which attracts to it the pabulum required for its nutrition, so that the interstitial waste which is consequent on its use may be made good.

The nucleus is also an active constituent of the cell, and in young cells is proportionately larger than when the cell is matured. It is doubtful if it plays a special part as a centre of attraction in secretion, or in the nutrition of the cell generally, an office which is most probably discharged by the protoplasm; but it undoubtedly acts as a centre for its own nutrition. Numerous observations, moreover, clearly prove the truth of the generalisation originally propounded by Martin Barry, and confirmed by Goodsir, that the nucleus is intimately associated with the production of young cells. The karyokinetic phenomena which have been observed during the last fifteen years have established this on a firm basis, beginning with the original segmentation of the yelk and nucleus within the ovum down to the latest period of cell formation.

But, along with the karyokinetic changes within the nucleus and its cleavage, there is also a cleavage of the protoplasm of the cell, so that the daughter cell consists of portions of both the nucleus and the protoplasm of the mother cell. The question therefore has been put whether the division of the protoplasm is a consequence or a coincidence of the division of the nucleus. I am inclined to think that the cleavage of the cell protoplasm is consequent on the nuclear changes; for it must be kept in mind that certain of the movements in and rearrangement of the chromatin fibres of the nucleus precede any rearrangement of particles in the cell protoplasm so far as yet observed, and, still more, the process of cleavage. Applying, therefore, to the cell the well-known economic principle of division of labour, and that differentiation of structure carries with it differentiation of function, I regard the protoplasm as the nutritive and secreting element of the cell, and the nucleus as its primary reproductive factor.

The present position of the CELL THEORY differs therefore in many important respects from the doctrine advocated by Schwann and his immediate successors. Cells are no longer regarded as of necessity bladders or vesicles. A cell wall is not constant but of secondary formation. A free formation of cells within an extracellular blastema by deposition around a nucleolus to form a nucleus, and then around the nucleus to form a cell, does not take place. Young cells arise from a parent cell by division of the nucleus, followed by cleavage of the cell protoplasm, so that each cell is directly descended from a pre-existing cell. Although in so many of its details, therefore, the theory of Schwann has been departed from, yet the great generalisation of the cellular structure of plants and animals holds good, and his work will continue to mark an epoch in the progress of biological science.

The study of the very remarkable series of karyokinetic phenomena above described has given an impulse to speculation and thought in connection with some of the most abstruse problems of Life and Organisation. The question of the hereditary transmission of properties, both as regards the constituent tissues of the organism and the individual as a whole, has been put on a more definite physical basis. The penetration of the ovum by the spermatozoon, originally seen by Martin Barry in the rabbit, and extended to other animals some years afterwards by Newport, Bischoff, and Meissner, has been completed by the recent researches of Bütschli, Auerbach, Fol, Hertwig, and E. van Beneden. The conjugation or incorporation of the male pronucleus or head of the spermatozoon with the female pronucleus derived from the germinal vesicle, and the consequent formation of the segmentation nucleus, has been demonstrated. The segmentation nucleus is built up of chromatin fibres and nucleoplasm, derived from both the nucleus of the male sperm cell or the spermatozoon and the nucleus of the female germ cell. It is therefore a composite or hermaphrodite nucleus, and represents both parents. The cells derived from the segmentation nucleus in the early stage of segmentation contain chromatin nuclear particles, which are in direct descent from the chromatin fibres of the segmentation nucleus, and through it from the corresponding fibres of both the sperm and germ cells. From Nussbaum's and E. van Beneden's observations it would seem that each nucleus of the first pair of segmentation cells contains one-half of the chromatin threads of the male, and one-half of those of the female pronucleus. It is possible that an equal division of the male and female components of the nuclei takes place in every subsequent nuclear division, in which case the nucleus of every cell would be hermaphrodite or composite, that is, would represent both parents. The segmentation cells arrange themselves to form the blastoderm, which, in the more complex organisms, by the continuous subdivision of the cells, forms three layers; from which, by a prolonged process of cell division and differentiation, all the tissues and organs of the adult body are ultimately derived. Karyokinetic changes mark the process of cell division throughout, and each daughter cell receives from the mother cell chromatin nuclear material derived from both parents, which, without doubt, conveys properties as well as structure.

In the division of the segmentation nucleus within the ovum a cleavage of the protoplasm of the egg also takes place, and each daughter nucleus is enveloped by the protoplasm of the maternal egg. If during the period of nuclear division there is no interchange of matter between the nucleus and the protoplasm which incloses it, the cell protoplasm would then be derived solely from the ovum, and would represent maternal characters only, whilst the nucleus would possess characters derived from both parents. But if, as is most likely, during the process of karyokinesis, when the nuclear membrane has disappeared, an interchange of matter takes place between the nuclear substance and the cell protoplasm, the latter would then become, if I may say so, inoculated with some at least of the nuclear substance, and be no longer exclusively of maternal origin. Again, it should be stated that, as E. van Beneden has described, when the spermatozoon enters the egg it takes with it a portion of the protoplasm of the sperm cell. This apparently blends with the protoplasm of the egg itself. With Waldeyer, therefore, I would ask the question, Is this altogether without significance? It would seem, therefore, as if the whole of the cells of the body and the tissues derived from them are, as regards both nucleus and cell protoplasm, descended from material originally belonging to both parents.

Although ova in different organisms differ materially from each other in size, shape, the relative amount of food yolk which they contain, the mode of segmentation, and the presence or absence of a segmentation cavity, they all agree in this that the primordial cells of the egg are nucleated masses of protoplasm. Notwithstanding, the general resemblance of the morphological units which thus mark the first stage in the production of young organisms, each fertilised ovum gives rise to an organism resembling that in which the egg itself arose. Hence the offspring resemble the parents, and the species is perpetuated by hereditary transmission, so long as individuals remain to keep up the reproductive process. During sexual reproduction the substance of the segmentation nucleus undergoes karyokinetic changes during the act of segmentation, and the question arises if the process of karyokinesis is the same for all organisms, whether plants or animals, or if there are specific differences. As the fertilised ovum is potentially the organism which is to arise from it, specific differences not unlikely exist in the minute structure of the segmentation nucleus, which may be expressed by modifications in the arrangement of the chromatin fibres and in the number of their loops. The varieties which have been described in the forms of the karyokinetic figures and polar radiations in different plants and animals may perhaps mark these specific differences.

But there is another question which merits consideration. Are the karyokinetic phenomena which show themselves in the cells of a given tissue characteristic of that tissue; and, if so, would it be possible to distinguish one tissue from another in the same organism by differences in the process of cell division? On this point a commencement seems to have been made towards obtaining some positive knowledge. Strasburger and Heuser think that they have obtained evidence in certain plant cells that such is the case; Rabl concludes, from observations on the epidermic cells of Salamander, that the loops of chromatin fibres are constantly twenty-four in number in the same kind of cell in the same species of animal.

But in considering the different kinds of tissue, and the possibility of each kind possessing its characteristic karyokinetic process, it has to be kept in mind that more than one kind of tissue, each of which has its characteristic structure and function, arises from each layer of the blastoderm, so that there is a stage in development—a stage of indifferentism, if I may use the expression—when the blastoderm represents several tissues which have not yet differentiated. From the epiblast, for example, tissues so diverse in structure and function as cuticle and nerve tissue arise. Now, if there be a special karyokinetic process for the epidermal cells, and another for the nerve cells, does either of these correspond with the process of nuclear division in the cells of the epiblast in their stage of indifferentism, or do they both differ from it? When does the impulse reach the layers of the blastoderm, so as to produce in their constituent cells changes which so alter the characters of the cells as to lead to a differentiation into various forms of tissues, and to what is that impulse due? In the development of each species there seems to be a definite time within certain limits when the differentiation shall begin, and when the process of development of the tissues and organs shall be completed. This is an hereditary property, and is transmitted from parents to offspring. Is the impulse derived from the nucleus or from the cell protoplasm, or do both participate? As already stated, the nucleus is the element which is immediately descended from both parents, and which may therefore be supposed to be the primary, morphological unit through which hereditary qualities are transmitted. But, as is most probable, the nucleus reacts on the cell protoplasm—on the element of the cell through which the ordinary nutritive functions are discharged. As a consequence of this reaction when the appropriate time arrives in the development of each species, for the commencement of the differentiation of the protoplasm of a cell, or group of cells, into a particular kind of tissue, the necessary morphological, chemical, and physiological changes take place. When once the differentiation has been effected, it is continued in the same tissue throughout the life of the organism, unless through some disturbance in nutrition, the tissue atrophies or degenerates. Every multicellular organism, in which definite tissues and organs are to arise in the course of development, has therefore a period, varying in its duration in different species, in which certain of the properties of the cells are as it were dormant. But, under the influence of the potent factor of heredity, they are ready to assume activity as soon as the proper time arrives. When the process of differentiation and development is at an end, the organism has attained both its complete individuality as regards other organisms, and its specific characters.

Every organism, therefore, has to be viewed from both these points of view. Its specific position is determined by that of its parents, and is due to the hereditary transmission of specific characters through the segmentation nucleus. Its individuality is that which is characteristic of itself; and arises from the fact that in the course of development a measure of variability within the limits of a common species, from the organic form exhibited by its parents and by their other offspring, is permitted. In all likelihood the variability, as Weismann has suggested,[1] is, to a large extent, occasioned by the bisexual mode of origin of so many organisms. By the expulsion of the polar bodies, during the maturation of the egg, portions of the ancestral germ plasm may be removed, and as corresponding molecules need not be expelled from each ovum, similar ancestral plasms would not be retained in each case, so that diversities would arise. There is also a possibility of the molecular particles of the segmentation nucleus and of the nuclei of the cells descended from it, having a method of arrangement and adjustment, and a molecular constitution characteristic of the individual as well as of the species. On this matter we have, however, no information. It is as yet a mere hypothesis. When we consider the extreme minuteness of the objects referred to, and recollect that it is only about fifteen years since karyokinetic phenomena were first recognised, it is astonishing what progress in knowledge has been made within this limited period. We owe this great advance to the much more complete magnifying and defining power of our microscopes, to the improved method of preparation of the objects, and to the acute vision and clear-thinking brains of those observers who have worked at the subject. By continuing the work, and extending it over a wider area, we may hope in time to be able to solve many questions to which we cannot now give an answer.

The nuclear material which makes up the substance of the male and female pronuclei, by the fusion of which the segmentation nucleus is formed, has been termed by Professor Weismann the *germ plasm*. In a series of elaborate papers he has developed a Theory of Heredity,[2] based upon the supposed continuity of the germ plasm. He believes that in each individual produced by sexual generation a portion of the germ plasm derived from both parents is not employed in the construction

[1] See his Essays "The Significance of Sexual Reproduction in the Theory of Natural Selection;" "On the Number of Polar Bodies and their Significance in Heredity;" translated in *Essays on Heredity*, Oxford, 1889.

[2] Translations of these papers have been published by the Clarendon Press, Oxford, 1889.

of the cells and tissues of the soma, or personal structure of that individual, but is set aside unchanged for the formation of the germ cells of the succeeding generation—that is, for reproduction and the perpetuation of the species. According to this theory, the germ plasm, more especially through the chromatin fibres, is the conveyer of hereditary structure and properties from generation to generation. Further, he holds that the cells, tissues, and organs, which make up the somatic or personal structure of the individual, exercise no modifying influence on the germ or reproductive cells situated in the body of that individual, which cells are also, he thinks, unaffected by the conditions, habits, and mode of life. In its fundamental idea Weismann's theory is in harmony with one propounded a few years earlier by Mr Francis Galton.[1]

In an address delivered at Newcastle in September last to the Anthropological Section of the British Association,[2] I reviewed this theory of heredity, and, whilst finding in it much with which one could coincide, I directed attention to points to which, I thought, objection might be taken. More especially I took exception to the idea that the germ plasm was so isolated from the cells of the body generally as to be uninfluenced by them, and to be unaffected by its surroundings.

On this occasion I propose to say a few words on the bearing of this theory on the development of the tissues and organs of the individual. If we examine the development of the embryo, say of one of the Vertebrata, we find that it makes a certain advance, varying in its time and extent according to the species, without any differentiation of a reproductive organ with its contained germ plasm being discoverable. I shall not enter into the much-disputed question of the layer or layers of the blastoderm from which the reproductive cells take their rise. But I may say that in the Chick, both in the third and fourth day of incubation, a layer of germinal epithelium may be seen in close relation to the Wolffian duct and the pleuro-peritoneal cavity. At the end of the fourth day or in the fifth

[1] *Proc. Roy. Soc. London*, 1872; and *Jour. Anthrop. Inst.*, vol. v., 1876.

[2] This address was reported at considerable length in the *Times* newspaper, September 14th, and in full in *Nature*, September 26th. It will also appear in the reports of the Newcastle meeting published by the Association.

day this epithelium becomes thickened, and the primordial ova appear in it as distinctly differentiated cells. In the Rabbit a corresponding differentiation does not appear to take place before the twelfth or thirteenth day. Up to the period of differentiation of the primordial ova, no isolation or separation of the reproductive cells and germ plasm has taken place; and, so far as observation teaches, there is nothing to enable one to say which cells of the blastoderm may give rise to primordial ova, or which may differentiate into cells for other histiogenetic purposes. But before the germ cells appear, the rudiments of the nervous, vascular, skeletal, muscular, tegumentary, and alimentary systems, and the Wolffian bodies or primordial kidneys have all been mapped out. Up to this time, therefore, in all probability, a more or less complete diffusion of the germ plasm throughout either one or more of the layers of the blastoderm has taken place. The hereditary influence conveyed by the germ plasm would thus be brought to bear upon the cells of the blastoderm generally, so as to impart to them the power of undergoing at the appropriate period the morphological and chemical differentiation to form the several tissues. As the tissues and organs are derived through division of the nuclei from the cells of the blastoderm, the continuity of the hereditary influence exercised over them is kept up, even after the germ plasm has become isolated, and the entire organism is moulded so that it acquires its specific and individual characters.[1]

[1] On the question of the influence exercised by the germ plasm on the tissues, I may refer to some most suggestive remarks by Sir James Paget, published forty years ago, in the *London Medical Gazette*, 1849, in one of his Lectures (VI.) on "The Processes of Repair and Reproduction after Injuries:"—"In every impregnated germ we must admit that properties are implanted, which, in favourable conditions, issue in the power to form, of the germ and the materials it appropriates, a being like those from which it sprang. And, mysterious as it may seem, yet must we conclude that a measure of those properties is communicated to all the organic materials that come within the influence of the germ: so that they, being previously indifferent, form themselves in accordance with the same specific law as that to which the original materials of the germ are subject. So through every period of life the same properties transmitted and diffused through the whole organism are manifested in the determination of its growth and maintenance, in its natural degeneration, and its repair of every part, in accordance with that type or law which has prevailed in every individual of the species." See also a Lecture "On the Formative Process," in *Lectures on Surgical Pathology*, vol. i., London, 1853.

But the diffusion of the germ plasm throughout either the whole of the blastoderm, or a part thereof, of necessity so intimately associates it with the formative cells of the tissues generally, that it is difficult, if not impossible, to comprehend how in its turn it can be unaffected by them. Before, therefore, it again becomes stored up or isolated in an individual, in the form of ova or sperm cells, it has in its stage of diffusion been brought under precisely the same influences as those which in the embryo affect the formative cells of the whole body.

From the observations and reasoning of Wilhelm His,[1] there can, I think, be no question that the layers of the blastoderm are affected by pressures and other mechanical conditions. These pressures would produce or modify flexures, or occasion a diminution in dimensions in some directions and an increase in others; and in this way would tend to affect either the form of the entire organism, or the form and relations of its constituent parts, or perhaps both. Should such modifying influences come into operation either before the isolation of the germ plasm, or when it was in a plastic or impressionable condition, one could conceive that it might be affected by them. Molecular changes might thus be induced in the germ plasm of such a kind as to modify the properties of the chromatin constituent of the nuclei, so as to induce in it and the germ plasms descended from it corresponding modifications, which would become hereditary. If such an hypothesis be granted, it would follow that the external conditions would exercise a perceptible influence on the germ plasm of the reproductive cells, both in the individual in which they first manifested their effect and in the generations which are descended from him.

If the germ plasm, from the first stage of development of each organism, were completely isolated from the cells from which all the other cells of the body were produced, it would be possible to conceive its transmission from generation to generation unaffected by its surroundings. But as in each individual a stage of diffusion or non-isolation precedes that of differentiation into the special reproductive apparatus, it follows that the conditions which would secure the germ plasm and the

[1] *Proc. Roy. Soc. Edin.*, April 2, 1888.

soma cells from mutual interaction are not complied with. On this ground, therefore, as well as for the reasons previously advanced in my Newcastle Address on Heredity, I am unable to accept the proposition that there can be no transmission to the offspring, through the reaction of the soma on the germ plasm, of characters which may be acquired under direct external influences. But in questioning the accuracy of the proposition that somatogenic "acquired characters" are incapable of being transmitted, I do not of course contend that all the characters which may be acquired during the lifetime of an individual are perpetuated in his descendants.

Gentlemen! Well nigh fifty years ago great men, who were engaged in microscopical research, lived in this city and were connected with this school of medicine. Men who were leaders in biological discovery and modes of thought. Although we cannot claim to be in direct physical continuity with their germ plasm, and with the chromatin fibres of their nuclei, we are in the line of succession to their scientific heritage. It becomes us therefore to strive to make ourselves worthy of this great inheritance. If the members of the Society can in the course of years, by the excellence of their work, make advances in science at all comparable to those effected by these distinguished predecessors, we and those who come after us may then say, in all confidence, that the founders of the Society were justified in their endeavours to give it a place amongst scientific societies in Scotland.

2

REPRINTED FROM

THE QUARTERLY JOURNAL OF MICROSCOPICAL SCIENCE.

Sedgwick's Theory of the Embryonic Phase of Ontogeny as an aid to Phylogenetic Theory.

By

E. W. MacBride, B.A.,

Fellow of St. John's College, Cambridge; Demonstrator in Animal Morphology to the University of Cambridge.

In a recent number[1] of this Journal there appeared a paper by Mr. Adam Sedgwick on the significance of the embryonic phase in development, which embodies a principle which, if true, seems to me well fitted to throw light on some obscure problems in morphology.

It is not the object of the present essay to discuss the correctness of Mr. Sedgwick's views, but rather, assuming them to be true, to point out some of their consequences.

These views may be briefly stated as follows. Making a broad survey of the facts of ontogeny, we find that there are two main types or phases of development—the larval and the embryonic. In the former case the immature organism pursues a free life, engaging in the struggle for existence; in the latter case the developing animal is shut off from the influence of external conditions, either inside an egg-membrane or in the uterus of the mother; but in both cases it is relieved from the necessity of having to seek its own living, since nourishment is provided for it either in the shape of food-yolk or fluid nourishment exuded from the uterine walls.

In many cases the whole course of the ontogeny of an animal

[1] "On the Law of Development commonly known as von Baer's Law; and on the Significance of Ancestral Rudiments in Embryonic Development," 'Quart. Journ. Micr. Sci.,' April, 1894.

is embryonic, but in every case larval development is preceded by a longer or shorter period of embryonic development.

The whole interest of the science of Embryology lies, of course, in the fact that features observed in both types of development seem inexplicable except on the assumption that they are reminiscences of structures possessed by the ancestors of the animals in whose development they appear. Such traces of the history of the race are to be found in the vast majority of larvæ; in embryos they are likewise to be found, though here they are less prominent, as is seen by comparing the development of two allied forms, in one of which the larval type prevails, and in the other the embryonic. Now Mr. Sedgwick's theory of the relation of the two types to one another is that that portion of embryonic development in which ancestral features are observable represents a larval stage passed over inside the uterus or egg-membrane and modified in consequence. Thus the chick during the first four or five days of its existence is to be regarded as an immensely modified larva.

If this view be true it follows that, however modified the record of ancestral history contained in the larval development may be, the embryonic record of the same history can never rise above it in value.

It was until lately customary to assume, explicitly or implicitly, that there was an inherent tendency for the ontogeny of the individual to be a summarised repetition of the phylogeny of the race. In proof of this statement we may adduce Balfour, who in his 'Text-book of Comparative Embryology' (vol. ii, p. 298), says, "Unless secondary changes intervened this record [of ancestral history] would be complete;" and Bateson,[1] in his discussion of the ancestry of the Chordata, commits himself to a similar position. That there can be no such general tendency is, however, shown by the fact that in

[1] "The Ancestry of the Chordata," W. Bateson, 'Quart. Journ. Micr. Sci.,' 1886. "Development within an egg-shell as involving a less complicated struggle with enviromental forces, is less subject to variation than that in the open sea, and consequently is more likely to preserve ancestral features."

bud ontogeny there is no trace of anything which can be interpreted as ancestral structures, and that some most striking and recent changes, such as the loss of limbs in snakes or the reduction of the toes of the ostrich to two, are not recorded in embryology, i. e. the organ concerned shows from its inception the adult arrangement.

How then does the theory we have adopted account for the retention of ancestral characters by larvæ?

So far as we can judge by comparative anatomy, the stimuli to evolution (in the sense of change of structure) have been two, viz. (1) change of environment and habits, and (2) increased or decreased demands on the working of certain organs. As we therefore pass along a series of genetically connected animals, we should find, pari passu with the environment and the functional demands of the organism, the structure changing. If these stimuli commenced to act from the beginning of free life, then each individual adult in the chain would show from the beginning the modified structure belonging to it; but if these stimuli were deferred in their operation till the animal had attained a certain size, then what was before a uniform life-history would become differentiated into two periods—a larval during which the ancestral habits were retained and the structures corresponding to them, and an adult in which new habits were assumed and structure correspondingly modified.

An illustration will make this clear: if young flat-fish when they emerge from the egg were at once to adopt the adult mode of life, then that most interesting larval stage, in which they are bilaterally symmetrical, would be missed out in their development.

Thus we see as a race of animals progressed from point to point in evolution, it would tend to develop a trail of larval stages, each grade of development surmounted being represented by a new larval stage intercalated in the ontogeny. This process, however, could not go on indefinitely; there would soon arise the tendency for the earlier larval stages to be passed over whilst still in the egg-membrane, and so a portion of the development would become embryonic, and so subjected to the various modifying influences which are connected with this type of ontogeny. Therefore it follows, as the first important deduction from Sedgwick's theory, that in seeking to obtain a basis for phylogeny, most importance must be attached to animals which show long larval histories.

Balfour with his usual sagacity has, so to speak, instinctively anticipated this conclusion. Although he points out that "the favourable variations which may occur in the free larva are much less limited than those which can occur in the fœtus," he says that there is "a powerful counterbalancing influence tending toward the preservation of ancestral characters, in that larvæ are compelled at all stages of their growth to retain in a functional state such systems of organs at any rate as are essential for a free and independent existence" ('Comp. Emb.,' vol. ii, p. 299).

The objection, alluded to in Balfour's statement, that larvæ as well as adults have been subjected to the modifying influences of their environment, will readily occur to most minds. Let us consider whether it is possible to approximately estimate the nature and amount of such influences; and, first of all, let us consider what is meant by secondary larvæ.

Balfour imagined that secondary larval forms might be produced by a diminution in the food yolk, and consequent earlier commencement of free existence (loc. cit., p. 300). There is no evidence to suggest that such a change has ever taken place; all the facts point in a contrary direction. We shall see that food yolk produces the most diverse distortions of development; the developmental processes of free larvæ are, on the other hand, remarkably uniform. Secondary larvæ must be regarded as having arisen owing to the young adults having taken to a new mode of life; the best instances of this are perhaps the aquatic larvæ of the may-flies and dragon-flies. We have the strongest reason for believing that the immediate ancestors of insects were terrestrial animals, and the aquatic larvæ mentioned show their secondary character by the fact that their respiratory organs are modified from organs adapted to air breathing. Their "tracheal" gills, instead of like all other gills bringing the blood into close proximity to the water, bring their blood first into contact with air contained in a system of closed tubes, and then this air into contact with the water.

In the case of ordinary larvæ, the probability of modifications due to adaptation to the environment cannot be denied. If, however, Sedgwick's hypothesis is correct that "larval history is constructed out of ancestral stages," or, in other words, that the larva retains ancestral characters because it retains the ancestral mode of life, then the environment has remained to a large extent constant (at any rate in the commonest case, that of pelagic larvæ), and the changes they are likely to have undergone, instead of being, as Balfour supposed, unlimited, will be comparatively few in number.

Of these changes reduction in size is the most important. The passage to the adult state is often accompanied by the loss of larval organs, and great changes in those which are retained, necessitating in some cases the complete destruction of their constituent cells, and their reconstruction from rudiments which have retained the embryonic condition (histolysis). It is, therefore, clearly to the advantage of the larva to grow no larger than necessary before it undergoes metamorphosis. Correlated with this loss of size is the frequent disappearance of all traces of segmentation, since this is probably to be regarded as essentially the same phenomenon as vegetative reproduction, only held in check by the individuality of the whole. Metameric series of organs are represented only by those members which are absolutely necessary. Another change which larvæ are prone to undergo, is the acquisition of transparency. What results this carries in its train will be mentioned below. Finally, the occurrence of long spines is a widespread phenomenon, though what their precise use is it would be rash to surmise. Possibly they are of a protective nature.

Let us now apply these principles in a concrete case, for example the larvæ of the Crustacea.

The characteristic larva of the Entomostraca is the well-known Nauplius, which shows no signs of segmentation. We have however from comparative anatomy, strong reason for believing that the ancestor of the Crustacea was segmented, and that it was probably related to the Polychæta. How is this apparent contradiction to be explained? We answer that the Nauplius retains the ancestral habits of Crustacea, and with this a certain necessary amount of ancestral structure; but it has diminished in size and external segmentation has disappeared. Since in the ancestor locomotion and prehension of food were effected by one or two pairs of anterior appendages only, we have these alone represented in the Nauplius, though the ancestor doubtless possessed in addition a series of segments bearing undifferentiated parapodia-like appendages. The complete disappearance of these is a mark of the high specialisation of the larva; if we compare the various families of the Entomostraca with one another, we find that in the primitive group of the Branchipoda, the Nauplius shows indications of a postoral segmentation; whereas in the highly specialised Cirripedes and Ostracods we get a specialised Nauplius. In the former case this is brought about by the outgrowth of great spines, in the latter by the precocious appearance of the adult bivalve shell, and in neither instance is there a trace of segmentation.

The larva of the Malacostraca the Zoæa, has been a great puzzle to morphologists. It is quite impossible to regard some of the peculiar features, such as the suppression of the thoracic segments and their appendages, as ancestral, and the question has been raised by Claus,[1] whether it has any phylogenetic significance at all.

Applying Sedgwick's principle, we explain the Zoæa as representing a later ancestral stage than the Nauplius, in which some of the Nauplius appendages had become exclusively masticatory and others exclusively tactile in function; the main locomotor function had been, so to speak, passed on to the two or three pairs of maxillipedes, which are

[1] L. Claus, "Zur Kenntniss d. Malakostrakenlarven," 'Würz. Naturw. Zeitschrift,' 1861.

always large and biramous, whilst at the same time some of the most posterior segments have been modified to form a powerful jointed "tail." The thorax retained its primitive character, and is accordingly suppressed in the larva; though here in comparing the Zoeæ of the various groups we meet with a precise parallel to the case of the Nauplii. The Zoæa of the undifferentiated Schizopod possesses only one pair of maxillipedes, and even they are short and somewhat foliaceous, but it shows a distinct segmentation of both thorax and abdomen. Still more instructive are the larvæ of the lower families of the Decapods, the Sergestidæ and Penæidæ. Taking Penæus for example, we find that it escapes from the egg-membrane as a Nauplius: it gradually changes to a Zoæa with two pairs of maxillipedes and the thorax distinctly segmented and with rudimentary appendages; this passes into a form with thorax well developed and all its appendages biramous—the so-called Mysis-stage, closely resembling the adult Schizopod,—and from this it passes to the adult state. On the other hand, in the highly specialised Brachyura we find a highly specialised Zoæa, in which the thoracic segments are totally suppressed and the thorax prolonged into great spines, the Mysis-stage is dropped but a new "Megalopa"-stage is introduced, which strongly recalls the Macrura, and may be taken to indicate a Macrurous ancestor. The existence of the Megalopa and Mysis stages, the significance of which is obvious, affords the strongest reason for maintaining the ancestral significance of the Nauplius and Zoæa stages; in doing so one merely follows the universal rule of science, i. e. reasoning from the known to the unknown.

Turning now to the embryonic type of development, let us examine the causes which are likely to modify a course of development which is primitively larval. First we must discriminate between various kinds of embryonic development. There is, in the first place, the type in which the organism is confined within the egg-membrane and supplied with nutriment by means of yolk stored up in its cells. Secondly, we have cases in which the embryo, still remaining in the egg-membrane, is retained in the body of the mother, the egg being closely applied to the uterine wall, from which nourishment is obtained, and the yolk having consequently in large measure disappeared. Thirdly—a much rarer case,—a number of eggs are enclosed together in a capsule and only one develops; the eggs destined to be eaten being known as yolk cells. As a less extreme case we have the eggs all developing up to a certain stage, but only a few surviving. This condition is seen in Prosobranch Mollusca. Lastly, we may mention those cases in which the uterus or other brood-pouch of the mother is used, so to speak, as a nursery for the larvæ, the embryos escaping from the egg-membrane, and passing the earlier part of their existence as free-swimming organisms inside the brood-pouch.

Taking the first case, which is by far the commonest, the disturbances of development which are found in it are due to two main causes—yolk and the egg-membrane. It is owing to the cramping influence of the latter that external differentiation of form is to a large extent lost. The gastrula of Asterina gibbosa, for instance, is almost spherical, contrasting thus with the common form of Echinoderm gastrula, which is more or less elongated. Where the egg is enclosed in a roomy capsule, on the other hand, as in the Pulmonata, this is less frequently the case; for instance, we have the velum of Limnæus and Planorbis. Mere disuse will not suffice to account for the disappearance of external organs, as in this case all traces of ancestral history ought to disappear in internal as well as external organs, and this is not the case.

The presence of food yolk exercises the most distorting influence on development. To Lankester[1] is due the credit of first laying emphasis on this. In treating of the development of Mollusca he points out that the question whether the endoderm is represented by many or few cells, and whether, consequently, these are invaginated to form the gut, or whether the ectoderm grows over them, is entirely determined by the amount of yolk present. Balfour, who had almost at the same time instituted a

[1] "On the Invaginate Planula or Diploblastic Phase of Paludina vivipara," E. Ray Lankester, 'Quart. Journ. Micr. Sci.,' vol. xv, 1875.

similar comparison between the segmentation of the eggs[1] of vertebrates, subsequently put forward the thesis,[2] based on a comprehensive survey of the facts of embryology, that the rapidity of segmentation of a given region of the ovum is inversely proportional to the amount of yolk contained in it.

The general effect of the presence of yolk, therefore, when massed specially in the endodermic end of the ovum, is to impede cell division, and render processes of development which depend on folding (e. g. invagination) impossible.

There is, however, another manner in which yolk can be accumulated, and that is in the more central portion of the ovum, instead of at one end. This is characteristic of the Arthropoda. When it is comparatively moderate in quantity, as in the case of Lucifer, segmentation and invagination can proceed normally, though the number of cells composing the blastosphere is small. When it is somewhat greater in quantity, as in Branchipus, segmentation at first proceeds normally, but soon the inner yolky ends of the blastomeres fail to be governed by the rapidly increasing nuclei, and segmentation only affects the outer layer of the egg, the inner ends of the first formed blastomeres fusing together to form a central yolky mass. In most Crustacea the yolk is so large in quantity that only superficial segmentation is possible from the beginning. Invagination of this outer layer to form the gut still occurs in some cases, the yolky mass being pushed before it; but, since the yolk is eventually absorbed by the endodermic cells, even this soon ceases to be possible, and we reach eventually a condition in which the segmentation and first processes of development recall to a certain extent those found in telolecithal eggs when the yolk increases to such an extent as to prevent segmentation at the endodermic pole at all (meroblastic eggs). In the scorpions and insects segmentation in its earlier stages is totally suppressed, and represented merely by the multiplication of nuclei; and in the later stages segmentation only occurs where developing organs require it, and thus a mimetic meroblastic segmentation is produced.

[1] 'Quart. Journ. Micr. Sci.,' 1875. [2] 'Comp. Emb.,' vol. i, p. 121.

The second type of embryonic development, viz. that in which the egg is applied to the uterine wall, is characterised by the reduction of the food yolk, so that the segmentation reverts to the total type. Sharply marked traces, however, of the former presence of yolk remain. The gorging of the endoderm with yolk has rendered the archenteron functionless, and as it still remains functionless when the plan of absorbing nutriment from the uterus through the general surface is introduced it is deferred in development, and in fact the destiny of the first products of segmentation is totally different in Mammalia from what it is, for example, in Echinoderms.

In the third type of embryonic development, in which the ovum is enclosed in a capsule with a number of yolk cells, the most weird changes are produced in development. We read of a complete separation and subsequent reunion of the blastomeres for instance; this type is almost confined to the Platyhelminths, and is alluded to here only for the sake of completeness, and to show how few traces of ancestral history the development of these animals affords. One family only, the Dendrocœla, lay their eggs singly, and in this case we have a large amount of food yolk present; yet Platyhelminths have bulked largely in many phylogenetic speculations.

Lastly, we have those few cases in which the developing animal escapes from the egg-membrane, but remains in the uterus or brood-pouch. In these cases we have comparatively little interference with the normal course of development. The early stages occur in a perfectly regular manner, and we have, in fact, free-swimming larvæ within the brood-pouch; it is only in the later stages that they commence to absorb fluid from its walls. It is necessary to emphasise this type of development, though it is comparatively rare (Brachiopods, Paludina, and Amphiura squamata) because if it is confounded with the foregoing types, its totally different characteristics would seem quite inexplicable.

I ought perhaps to mention that the earlier stages of Amphiura squamata are described as being abnormal by

Russo,[1] but neither the figures nor the methods of this author are calculated to inspire much confidence. These earlier stages are very difficult to obtain, but I have strong reason to suspect from those which I have seen, that the earlier development follows the ordinary Echinoderm type.

Having thus rapidly reviewed the principal disturbing factors in embryonic development, we can employ our knowledge in attacking one of the most vexed questions in morphology, viz., the significance of the mesoderm and its contained cavity the cœlom.

Is the former to be regarded as a differentiated portion of the gut-wall, and the latter as a portion of the enteric cavity, or is the cœlom to be regarded as a mere enlargement of the cavity of the gonad as Hatschek[2] has suggested?

In all Annelids and all Mollusca (Paludina and Cephalopods excepted) the mesoderm first appears as two symmetrically situated large cells—the primary mesoblasts. In Paludina, Echinodermata, Sagitta, Brachipoda, and Amphioxus, it arises as one or more pouches of the gut. Now, leaving out of account Anthropods, Vertebrates and Cephalopods, where the development has been complicated by the enormous amount of yolk present, we find that of the other groups the Echinoderms have by far the most prolonged larval development. They are unique amongst the Cœlomata in the fact that the blastosphere is a free-swimming larva, and that consequently the development of both endoderm and mesoderm takes place during their free-swimming life. Here, then, we may on our hypothesis expect to find ancestral structure preserved, and here we find that the cœlom is developmentally a part of the archenteric cavity.

No Annelid or Molluscan larvæ commence free life so early; most of them may be ruled out at once for the purposes of this comparison, since the disturbing presence of yolk shows itself plainly in the fact that the endoderm is represented by a few large spheres, and the production of a pouch has become

[1] Achille Rosso, "Embryologia d' Amphiura squamata," 'Rendiconti della Società Reale di Napoli,' tome vii (2nd series).

[2] 'Lehrbuch der Zoologie,' 1891, B. Hatschek.

an impossibility. A few Annelid eggs have, however, very little yolk, and the larvæ commences a free life in the gastrula stage.[1] Even here, however, if the blastosphere be compared with that of an Echinoderm, one is struck at once by the comparatively small number of cells it has, and one understands why the mesodermal rudiment should be represented by a single cell. The small number of cells is doubtless due to the comparatively large quantity of yolk, even if it be fairly uniformly distributed. This is probably, however, not the only reason why the cœlomic gut pouch is not found in the Annelid larva. If we compare Echinoderm larvæ with one another, we find that the blastocœle or segmentation cavity and the cœlom vary inversely with regard to one another. Thus in the creeping larva of Asterina the cœlom is very spacious, and the blastocœle reduced to a mere slit; in the pelagic larva of Asterias, on the other hand, the blastocœle is exceedingly large, and the cœlom has the form of two narrow tubes the lumen of which is in parts occluded. A similar comparison can be made between the ordinary Tornaria larva of Balanoglossus and Bateson's larva. The reason of this difference is not far to seek. It is to the over-development of the blastocœle with its contained jelly that pelagic larvæ owe that transparency which is so invaluable to them; hence the great development of the blastocœle in pelagic larvæ and consequent feeble development of the cœlom.

Now whatever may be the functions of the cœlom in Echinoderms, in Annelids its main functions are excretion, and the production of the sexual cells. Of these the first is performed in the Trochophore (the characteristic Annelid larva) by the so-called protonephridium, and the second has, of course, no place in larval economy. Hence, if we regard the Trochophore as bearing somewhat the same relation to the Echinoderm larva as the Zoæa of the crab does to that of Penæus, we see why the cœlom should have been entirely suppressed and the mesoderm represented only by a few large cells.

[1] Compare figures given in Korschelt and Heider's 'Lehrbuch der Vergleichende Embryologie.'

Thus the cœlom appears to be, phylogenetically, simply a differentiated portion of the archenteron; when the lumen of the latter is small, and its walls are composed of only a few large cells, the mesodermic walls of the cœlom are represented by a single large cell on each side.

A little consideration will throw light on the reason why what we see to be probably the primitive mode of development should appear in Paludina Brachiopods and Amphioxus. In all these cases the yolk is exceedingly small in quantity and uniformly distributed; in the first two cases we have a pseudo-embryonic development—the fourth type mentioned above,—and of course in this case there are no pelagic conditions to require a suppression of the cœlom. Amphioxus has a long larval history. Sagitta, on the other hand, pursues a true embryonic development within the egg-membrane; but the yolk appears to be quite uniformly distributed, and hence its primitive character.

A second vexed question which naturally follows directly on that of the origin of the mesoderm, is the origin of the endoderm, and consequently of the gastrula itself. Echinoderm development suggests the idea that the ancestral form of metazoon was a sphere of ciliated cells, and that the archenteron arose through the specialisation of a portion of the surface of the sphere to fulfil digestive functions and its invagination into the anterior. This is the view adopted by Korschelt and Heider;[1] and it is, of course, the famous gastræa hypothesis of Haeckel.[2] On the other hand, contrary opinions have been put forward by Metschnikoff,[3] Lankester,[4] and Sedgwick.[5]

[1] 'Lehrbuch der Vergleichende Embryologie,' vol. i, p. 81. Heider showed experimentally that carmine granules were swept by the cilia to the posterior end.

[2] Haeckel, 'Studien der Gastraea Theory,' Jena, 1877.

[3] El. Metschnikoff, "Spongiologische Studien," 'Zeit. für wiss. Zool.,' Bd. xxxii, 1879.

[4] E. Ray Lankester, "Notes on Embryology and Classification," 'Quart. Journ. Micr. Sci.,' vol. xvii, 1877.

[5] A. Sedgwick, "The Development of the Cape Species of Peripatus, pt. iii," 'Quart. Journ. Micr. Sci.,' vol. xxvii, 1887.

Metschnikoff starts, like Haeckel, from the blastosphere or blastula as an ancestral form; he supposed it, however, to have become filled up by cells wandering in from the periphery. In the midst of these a digestive cavity was later developed, and finally the mouth was formed by the specialisation of the area through which food was taken in. Lankester, starting from the same form, supposes the inner ends of the cells of the blastula to have become differentiated so as to be specially digestive in function, and later that they became separated off as a special layer. The cavity of the blastosphere was thus the digestive cavity, and food at first taken in over the whole surface, was later taken in only at one point, and thus a mouth was formed.

Sedgwick, on the other hand, is inclined to start from a protozoon in which cell territories were non-existent, though many nuclei were present. He supposes that the gut originated as a digestive vacuole, and that the nuclei acquired a definite arrangement with regard to this vacuole and other organs, and thus tissues were constituted. Cell territories, in so far as they exist in the adult, he regards as due to secondary rearrangement of the protoplasm.

We have already pointed out that Echinoderm development tells strongly in favour of the view supported by Haeckel and Korschelt and Heider, and that Echinoderm development, from its almost exclusively larval character, is of the very greatest importance in deciding such a question. Its evidence is by no means solitary; the statement may be made that, in all Cœlomata without exception, when the yolk is feebly developed and evenly distributed we find the embryo pass through a blastula stage which is converted into a gastrula by invagination (cf. Leucifer among Crustacea, Polygordius and Serpula and many others in Annelids, Paludina and Chiton in Mollusca, Amphioxus and Cyclostomes in Vertebrata, &c.). The groups which constitute the chief support of Metschnikoff's theory are Sponges and Cœlenterata. We may leave the first entirely out of account, as it is quite possible that they constitute a distinct phylum to the rest of the Metazoa. In many Cœlenterates we start from a blastosphere, which is in some cases a free-swimming larva. This blastospere, however, becomes filled up by cells which wander in from the external layer; in most cases this seems to take place from one end of the somewhat elongated blastosphere, and in Aurelia this process is replaced by invagination. Now the important point to notice in these larvæ is that during their free-swimming life the gut is functionless; and this accounts for the fact that it is represented by a solid rudiment. A precise parallel to the difference between the endoderm of the Cœlenterate and Echinoderm larvæ may be found amongst the larvæ of the Ectoproct Polyzoa. In the pelagic larva of Membranipora (Cyphonautes), which has a long free-swimming life, we find a perfectly well-developed gut with mouth and anus; on the other hand, in the larva of Alcyonidium we have a stomach of yolky cells, an almost occluded œsophagus, and no intestine, whilst in that of Bugula the whole mesoderm and endoderm is represented by a solid mass of cells. These larvæ are developed from yolky eggs and take in no nutriment during their free life. I hold, therefore, that Heider[1] is perfectly justified in his statement that the ancestor of the Cœlenterata was "a ciliated, oval, free-swimming form, in which by invagination at the posterior end an archenteron was formed."

Lankester's view finds its chief support in the development of Geryonia. In fact, this form is the only known one in which such a process as he supposes to have taken place in the blastula ancestor appears in the ontogeny. Are there any reasons for regarding the development of Geryonia as specially primitive? I think we may fairly say none; but that on the contrary it shows manifest signs of its secondary character; the egg is yolky, and the development proceeds directly to the medusa form, the hydra form being suppressed. The most conclusive argument, however, against Lankester's hypothesis is that on his assumption the cavity of the blastosphere is identical with the cavity of the future gut. Now all recent investigations have gone to show that the blastocœle is the rudiment of the

[1] 'Lehrbuch der Ver. Emb.,' vol. i, p. 81.

blood system, and has no connection with the gut whatever. In many Cœlenterates the stage of the hollow blastosphere is missed out, and segmentation results in a "morula" of which the external layer is the ectoderm and the rest endoderm. I think we must imagine that in the development of Geryonia the shortening process has gone one step further, and that as a result of segmentation we reach at once the stage of the hollowed-out planula.

Sedgwick's hypothesis was suggested from a study of the embryos of Peripatus capensis. Their developmental history is, however, the very last place where one ought to seek for indications of the ancestral meaning of the earlier stages —at any rate if Sedgwick's own hypothesis as to the significance of the embryonic phase be correct. All species of Peripatus so far as is at present known are oviparous; in Peripatus Novæ-Zelaniæ, however, the eggs are large and yolky, and the development conforms to the ordinary centrolecithal type so characteristic of Arthropods—the peculiarities of which we have described above. In Peripatus capensis nutriment is supplied by the wall of the oviduct, and the yolk has in large measure disappeared, at any rate its more solid portions; but the development still bears the impress of centrolecithal segmentation, i.e., in the imperfect definition of the blastomeres. It is obvious one might with equal justice expect to find information as to the character of the ancestor of Metazoa in the eggs of mammals.

Let us now briefly rehearse the conclusions to which the foregoing discussions seem to point. The earliest well-marked larval stage which we have discovered is the blastula—a sphere of uniformly ciliated cells. This "animal Volvox," as Huxley[1] calls it, may be regarded as a protozoon colony, not in the sense of consisting of independent units any more than does Volvox, but rather in the sense of being built up by the repetition of a unit as a result of what Lankester[2] calls "eumerogenesis," just as is the colony of a Hydromedusan. At first all

[1] 'Anatomy of Invertebrates,' p. 678.
[2] Art. "Hydrozoa," 'Encycl. Brit.'

elements in the blastophere were alike in structure and function. Later, however, coincidently with its acquiring the capacity for moving in a definite direction, a change would take place: the form first became elongated, and it is interesting to observe that the free-swimming blastulas of both Echinocyamus and Eudendrium have this form; then the cells at the posterior end, being least favorably situated with regard to promoting the locomotion of the colony, and best situated for seizing food particles, since they are in a kind of backwater from the eddies produced by the ciliary motion of the rest, would become specially digestive; increase in their number could only take place coincidently with invagination if the form of the colony were to be preserved and at the same time the digestive cells were to remain in contact with the surrounding medium—and thus we have the archenteron formed. The cells at the anterior end, on the contrary, are in the best position for receiving stimuli from the outer world; and here we should expect the first sense-organ to appear, and it is just at this spot that we find the larval sense-organ of Conatula with its associated nervous tissue, and the still more primitive sense-organ of the Echinocyamus larva, this latter consisting of a thickened patch of ectoderm bearing stiff cilia, which take no part in locomotion. In the same place the apical plate or larval brain of the Trochophore is found, also bearing cilia or more probably sense hairs.

Metschnikoff's[1] great objection to regarding invagination as the primitive method of forming the endoderm was that the blastopore sometimes became the mouth and sometimes the anus. Sedgwick's suggestion, however, that mouth and anus were differentiated from a slit-like blastopore, seems to answer this difficulty. That a slit-like opening can be represented by two independent perforations is shown by Echinoderm development. Thus in Holothurians the larval mouth by a shift of position becomes the adult; in Asterids and Echinids, on the other hand, it is represented by a totally new perfora-

[1] "Vergleichend Embryologische Studien. (3) Über die Gastrula Einiger Metazoen," 'Zeit. für wiss. Zool.,' Bd. xxxvii.

tion. No one can suppose that the ancestral form gave up its old mouth and developed a new one; the change was one of size and relative position only. We must assume that the original mouth was a wide one, and that part is utilised by the larva and aborted in the adult.

The cœlom, as we have seen, arose as a specialised portion of the gut.

It is to be observed that the history we have just sketched is in accordance with that rule which seems to hold in all cases where we can by means of comparative anatomy show with reasonable probability that evolution has occurred, viz. that new organs never arise de novo, but by the differentiation of older organs. This rule seems, however, to me to be violated by supposing that either archenteron or cœlom arose as a split in a solid mass of cells. The history affords also an explanation of that rigorous separation of primary and secondary body cavities, the blastocœle or hæmocœle, and the cœlom, which all recent research has tended to emphasise. The first is, in fact, morphologically inside and the second outside the primitive blastosphere.

Lastly, the conception of the primitive metazoon as a colony of Protozoa is in accordance with that repetition of similar parts on which Bateson[1] has laid so much stress as one of the most marked characteristics of living things. We should recall also the high individuality acquired by colonies of Siphonophora, Polyzoa, and Ascidians.

[1] 'Materials for the Study of Variation,' W. Bateson, Cambridge, 1890.

ON THE

ORIGIN OF METAMERIC SEGMENTATION

AND SOME OTHER

MORPHOLOGICAL QUESTIONS.

BY

ADAM SEDGWICK, M.A.,
FELLOW AND ASSISTANT LECTURER OF TRINITY COLLEGE, CAMBRIDGE.

Reprinted from the 'Quarterly Journal of Microscopical Science' for January, 1884.

LONDON:
PRINTED BY
J. E. ADLARD, BARTHOLOMEW CLOSE,
1884.

On the Origin of Metameric Segmentation and some other Morphological Questions.

By

Adam Sedgwick, M.A.,
Fellow and Assistant Lecturer of Trinity College, Cambridge.

With Plates II and III.

In the following pages[1] certain hypotheses with regard to the evolution of segmented Triploblastica (Annelida, Arthropoda, Vertebrata), and some apparently unsegmented forms (Mollusca Brachiopoda, Sagitta, Balanoglossus) are suggested and discussed.

I have found it convenient to consider the Vertebrata specially in the latter part of the paper, because of the very pronounced views which are held at the present day with regard to their evolution.

The paper is divided into two parts. The first part deals with the evolution of certain organs; the second part with the evolution of the groups mentioned and especially with that of the Vertebrata.

My hypothesis concerning the origin of metameric segmentation has been in a sense anticipated by Lang. He regards the somites as derived from gut pouches such as are found at the present day in Turbellarians. It should be remembered that according to his view, the Turbellaria are specialised Cœlenterates. My view of the origin of Somites differs from

[1] A short account of the main points of this paper was communicated to the Cambridge Philosophical Society in November, 1883, and published in vol. v of the 'Proceedings' of that Society.

his in taking a simpler diploblastic form as the starting point for all the Triploblastica discussed.

Hubrecht in his recent paper on the "Ancestral form of the Chordata" has explained Lang's views and instituted some important comparisons between Vertebrates and Nemertines. I differ, however, from Hubrecht in taking a simpler form as my starting point.

I have purposely refrained from referring to the Turbellaria and other flat worms in this essay, because I cannot make up my mind as to whether they are degenerate Enterocœla or highly specialised Cœlenterata (without a separated cœlom). I am, however, very much inclined to the view that they are degenerate Enterocœla.

I have also avoided discussing the Echinoderms because, while their early development is easy to understand, the later stages and metamorphosis are not so intelligible.

My hypothesis with regard to the origin of the mouth and anus has, so far as I know, not been suggested before. I agree with Hæckel in regarding the blastopore as homologous with the primitive mouth of the gastræa.

I have attempted to explain the peculiar behaviour of the blastopore in a general way, in the first part of my paper. In the second part I again consider this question in connection with the Vertebrate blastopore. I dissent most strongly from the view that the Vertebrate mouth and anus are both secondary perforations, and not homologous with those of Invertebrates, e. g. Annelids. I regard them both as homologous with the corresponding structures in the other Triploblastica discussed.

But I have not been able to do justice to this part of my subject. I could only do so by reviewing critically the extensive literature on this subject, and by making a special investigation of the behaviour of the blastopore in animals with a prolonged larval life, and of the structures classed as primitive streaks, and this I have unfortunately been unable to do. I think that any such investigation would have valuable results.

I agree with Balfour in his view that the "concrescence" theory of the growth of the Vertebrate embryo is untenable. It seems to me that the advocates of that theory have mixed up three distinct embryonic structures, the mesoblastic bands, the primitive streak, and the ridges of the medullary groove.

The primitive streak is in most forms at first a median structure. I agree with the current view as to its nature as a rudiment of the blastopore, and I suggest a reason for its persistence.

I ought particularly to mention that I regard the Annelid-origin of the Vertebrata and Arthropoda as untenable. This will be obvious to anyone reading the following pages.

I offer no suggestion as to the phylogeny of Mesoblast. I agree entirely with the current view that it has arisen from both of the primary layers.

Mesenchyme is obviously merely precociously developing mesoderm, and is particularly developed in free larvæ.

Finally, I may add that I do not put forward these hypotheses in a dogmatic spirit, and that I fully recognise that theories dealing with the complicated facts of morphology can only have in most cases a very temporary value. The main idea of the comparisons discussed below first occurred to me some years ago, when investigating the development of the Vertebrate excretory organs; but they have received such striking confirmation from Hatschek's work on Amphioxus, and more recently from a study of the embryo of Peripatus capensis, that I have at length decided to publish them, hoping that they may at least excite criticism and so lead to the increase of our knowledge, and to the greater definition of our ideas.

In the discussion which followed the communication of the late Professor Balfour's notes and drawings of the early embryos of Peripatus Capensis, to the Royal Society (December, 1882), I drew attention to the great resemblance between the embryo of P. Capensis with its elongated blastopore and somites, and an adult Actinozooid polyp. I pointed out that the comparison of these two structures suggested an explanation, which so far as I know has not before been suggested, of a great morphological difficulty, viz. the origin of metameric segmentation (vide 'Nature,' December 28th, 1882). At the same time I pointed out that by following up this comparison some other morphological difficulties received an explanation.[1]

The hypotheses I suggested were shortly as follows;

1. The mouth and anus found in most of the higher groups (Vermes, Mollusca, Arthropoda and in all probability Vertebrata) have been derived from the mouth of an ancestor common to them and the Cœlenterata; i.e. from an elongated opening such as is found at the present day in the Actinozoa.

2. That the somites of segmented animals are derived from a series of pouches of the primitive gut (archenteron) of a Cœlenterate-like ancestor, i.e. from pouches generally resembling those found at the present day in Actinozooid polyps and Medusæ.

That the excretory organs or nephridia (segmental organs) of the higher animals are derived from specialised parts of these pouches which were in the supposed ancestor, as indeed they now are in many living Medusæ and Actinozoid Polyps connected peripherally with each other by a longitudinal canal (circular canal of Medusæ, perforations in mesenteries of Actinozoa,) and with the exterior by a pore[2] one for each pouch; further, that in the Invertebrata, e.g. Annelida, the longitudinal canal has been lost and the external pores retained, while in the Vertebrata the longitudinal canal (segmental or pronephric duct) has persisted and

[1] Mr. E. B. Wilson, who was present when this discussion took place at the Royal Society, and to whom I subsequently at Cambridge showed the specimens and drawings of the Peripatus embryo, informs me that the work (referring to Polyps) which he has since done at Naples has enabled him to give some additional evidence in favour of my views. As Mr. Wilson's observations are not yet published, I am unable to quote them here; but he informs me that his paper is in the press, and will shortly appear in the Naples 'Mittheilungen.'

[2] Vide Hertwig, 'Organismus der Medusen,' p. 39; and "Actinien," 'Jena Zeitschrift,' Bd. xiii.

retained its posterior opening into the alimentary canal while the external pores have been lost.

I now add to these three propositions a fourth.

4. That the tracheæ are not developed from cutaneous glands of a worm-like animal with well-differentiated mesodermal tissues (a view which on physiological grounds is hard to accept) but are rather to be traced back to simple ectodermal pits in the two-layered ancestor developed for purposes probably of aeration and represented at the present day in the Cœlenterata by the subgenital pits of the Scypho-medusæ, in the embryos of Arthropoda by the pits into the cephalic ganglia, and in the Vertebrata by the canal of the central nervous system.[1]

The essence of all these propositions lies in the fact that the segmented animals are traced back not to a triploblastic unsegmented ancestor but to a two-layered Cœlenterate-like animal with a pouched gut, the pouching having arisen as a result of the necessity for an increase in the extent of the vegetative surfaces in a rapidly enlarging animal (for circulation and nutrition).

The hypotheses are based upon the embryonic development of the respective organs in the Triploblastica and the structure of the living Cœlenterata; in other words, upon facts precisely of the same nature as those which have been used in tracing the evolution of the nervous and muscular tissues.

Before proceeding to discuss the facts upon which the hypotheses rest, I may be permitted again to point out that it is no part of my view to derive segmented animals direct from the Cœlenterata, but to derive both Cœlenterata and segmented animals from a common Cœlenterate-like ancestor, whose structure can only be elucidated by studying the anatomy and the development of the living Cœlenterates, and of the higher segmented animals.

[1] Sedgwick, "On the Original Function of the Canal of the Central Nervous System of the Vertebrata," 'Proc. of Cambridge Phil. Soc.,' vol. iv.

On the Homology of the Mouth and Anus with the Mouth of the Cœlenterata.

It will be generally admitted that the mouth and anus of the Annelida, Arthropoda, and Mollusca are homologous structures—i. e. that the mouth of an Arthropod is homologous with that of an Annelid, and with that of a Mollusc, and that the anus in each of these groups is homologous with the anus of the other groups. It is well known that the blastopore in these groups presents considerable differences in its relation to the mouth and anus. In one form it is directly converted into the mouth, in another into the anus; while sometimes it entirely closes up and gives rise to neither (for summary of facts vide Balfour 'Comp. Embryology,' vol. ii, pp. 281, 282). This variability, in the fate of the blastopore was first pointed out by Lankester.[1] It is very puzzling, and has led some morphologists to regard it as a structure which is not homologous in the different animals, and of no particular phylogenetic significance. It seems to me, however, that a little consideration shows that this view of the blastopore must be given up, and that there are very strong grounds for regarding the blastopore as homologous in every case,[2] and also as homologous with the mouth of the Cœlenterata. Before proceeding to discuss the main point of this section of my paper, I must definitely examine this question about the blastopore.

On the Blastopore.—Either the blastopore has an ancestral meaning or it has not. It seems to me that we have no right to assume that this or any other embryonic structure or process is without a phylogenetic significance until all other views have been shown to be untenable.

It is often said when any peculiar embryonic process is discussed

[1] "On the Coincidence of the Blastopore and Anus in Paludina." This Journal, 1876.

[2] It must be distinctly understood that the only groups referred to in the following paper are the Vertebrata, Annelida, Arthropoda, Mollusca, Balanoglossus, Brachiopoda and Sagitta. For the present, I leave the Platyelminthes and Echinoderms out of consideration. The special case of the Vertebrata will be considered in Part II.

from a phylogenetic standpoint that it is only the way in which the animal develops, and that it is waste of time to attempt to explain it. I cannot agree to accept such a view of any embryonic fact. If there is anything in the theory of evolution, every change in the embryo must have had a counterpart in the history of the race, and it is our business as morphologists to find it out.

I wish to point out that I am not discussing how the gastrula arose. I take as my basis the undoubted fact that gastrulæ have existed, and I am trying to show that a two-layered, gastrula-like animal was the ancestor of most living Metazoa.

I must, therefore, reject the view that the blastopore has no ancestral meaning.

What, then, is its ancestral meaning?

It seems to me that there is very strong evidence for the view that it is homologous with the mouth of the Cœlenterata.

In the first place the Cœlenterate mouth either arises as a result of invagination, the blastopore remaining as the mouth (Cereanthus, Pelagia), or as the result of perforation. In the Triploblastica similarly the blastopore either arises as a result of invagination or as a perforation. The method of development, therefore, coincides, and we thus have a strong reason for regarding them as homologous.

The second important point to be examined in determining homologies is the relation to other important structures. The relation of the Cœlenterate mouth and the blastopore to the alimentary canal and the nervous system can in most cases be determined; and in all cases in which it can be so determined, it is the same.

(1) The Cœlenterate mouth and the blastopore resemble each other in being the main communication by which the archenteric cavity or its rudiment communicates with the exterior.

(2) They resemble each other in always being perforations of the neural surface of the body.

With regard to the first of these agreements nothing need be said; it is a fact of little importance, as there are many other channels in the Cœlenterata through which the archenteron communicates with the outer world. The second agreement is of great importance; but before it can be of any value to us, we must be able to decide whether the neural surfaces of the Cœlenterata, Annelida, &c., are homologous. It will be generally admitted that the nervous systems of the Annelida, Arthropoda and Mollusca are built upon the same type; and that the ventral surface of the body is homologous in each of these three groups. The late Prof. Balfour put forward the hypothesis that the nervous system of these types was homologous with that of Cœlenterata. He says:

"In the first place it is to be noted that the above speculations render it probable that the type of nervous system from which that found in the adults of the Echinodermata, Platyelminthes, Chætopoda, Mollusca, &c., is derived, was a circumoral ring, like that of Medusæ, with which radially-arranged sense-organs may have been connected; . . . . Its anterior part may have given rise to supra-œsophageal ganglia and organs of vision; these being developed on the assumption of a bilaterally symmetrical form, and the consequent necessity arising for the sense-organs to be situated at the anterior end of the body. If this view is correct, the question presents itself as to how far the posterior part of the nervous system of the Bilateralia can be regarded as derived from the primitive radiate ring.

"A circumoral nerve-ring, if longitudinally extended, might give rise to a pair of nerve-cords united in front and behind,—exactly such a nervous system, in fact, as is present in many Nemertines (the Enopla and Pelagonemertes), in Peripatus and in primitive molluscan types (Chiton, Fissurella, &c.). From the lateral parts of this ring it would be easy to derive the ventral cord of the Chætopoda and Arthropoda. It is especially deserving of notice, in connexion with the nervous system of the above-mentioned Nemertines and Peripatus, that the commissure connecting the two nerve-cords behind is placed on the dorsal side of the intestines. As is at once obvious, by referring to the diagram (fig. 231 B), this is the position this commissure ought, undoubtedly, to occupy if derived from part of a nerve-ring which originally followed more or less closely the ciliated edge of the body of the supposed radiate ancestor." 'Comparative Embryology,' vol. ii, pp. 311, 312.

It seems to me that nothing can be added to make the case stronger. I only wish to make one addition to the hypothesis, and that is that the type of nervous system from which that of the above-mentioned groups has been derived was a broad ring round the mouth, in fact, more resembled the nervous system of Actinia in its general diffusion over the oral surface than the compact ring of the Medusa; the latter being a highly specialised part of this generalised nervous system, which has, however, in part persisted in the subumbrella plexus of ganglion cells described by Schafer and Claus. If this hypothesis is correct, i. e. if it be true that the oral surface of a Cœlenterate is homologous with the ventral surface of the mentioned groups; and if the nerve-ring of the Medusa, the nerve-ring of Peripatus, the nerve-ring and general ventral nervous plexus of Chiton and Proneomenia, the cerebral ganglia and ventral nerve-cords of other Mollusca[1] and Annelida and Arthropoda are all derived from a general peri-oral nervous system of a Cœlenterate-like ancestor, then the relation of the blastopore to the nervous system is the same in the Annelida, Arthropoda and Mollusca and the same as that of the mouth of Cœlenterata.

With these facts before us, viz. similarity in development and in relation to other important structures, I think we can hardly doubt the fact that the blastopore in the cases mentioned and the Cœlenterate mouth are homologous structures.

In the above discussion I have avoided referring to the ultimate history of the blastopore. The fate of the blastopore in the Tripoblastica is extremely variable, and it is this variability only which has caused the homology ever to be doubted.

But I think we have here two distinct questions: one deals with the blastopore or mouth of the two-layered stage in

[1] The absence of the connection dorsal to the anus in some Mollusca, Annelida, and Arthropoda, will not I think be regarded as a fact of any importance if the hypothesis be accepted with regard to the nervous system of Peripatus and Chiton.

embryonic development and asks whether that stage has a counterpart in evolution; the other deals with the subsequent development of the blastopore and asks whether that subsequent development throws any light on the evolution of the mouth and anus.

But at the same time I must admit that the fate of the blastopore is so peculiar, that the doubts which on that account have been expressed as to its phylogenetic meaning are not unreasonable. The case stands thus. The blastopore in Serpula gives rise to the anus; in most other Chætopoda to the mouth; similarly in the Mollusc Paludina it becomes the anus, while the general rule among Mollusca is that it should become the mouth. It would seem to follow from these facts, as Lankester has already pointed out, that if the blastopore is in each case homologous, then the anterior end and mouth of Serpula must be homologous with the posterior end and anus of other closely allied Chætopods. This is manifestly absurd. There are two ways out of the difficulty; either the homology of the blastopore must be given up, or we must suppose that primitively it gave rise to both mouth and anus, and that its specialisation as a larval organ has caused the variability of its subsequent history. The latter view is obviously suggested by the elongated form the blastopore first assumes in many animals, extending as a slit along the whole of the ventral surface of the embryo.[1] The blastopore never retains for long this form, but soon becomes specialised to a round opening, the definite blastopore,[2] by the closure of the lip of the slit except at one point. The point at which it remains open must depend on the shape of the larva, &c., and will obviously be determined by the convenience of the larva.

This hypothesis that the mouth and anus of the Triploblastica is derived from a single opening, represented in living animals by the Cœlenterate mouth and, on the assumption

[1] This fact was first pointed out by Lankester, vide this Journal, vol. xvi, 1876, p. 326.

[2] A special name is wanted for this structure, to distinguish it from the blastopore of the gastrula stage.

(vide above p. 49) that the latter and the blastopore of higher types are homologous, by the early blastopore (before specialisation as the larval mouth) receives very strong support from the actual structure of the Actinozooid mouth, and from the newly discovered facts with regard to the history of the blastopore of Peripatus capensis; and has the merit of being on a priori physiological grounds easily conceivable.

Mouth of the Actinozoa.—In the Actinozoa the mouth-opening is elongated, and the animal is symmetrical on each side of the long axis of the mouth. At one end of the long axis the mouth is especially differentiated, and this differentiation extends down the stomodæum as a strongly ciliated groove called by Hickson[1] the Siphonoglyphe. The cilia of this groove produce a current from without inwards, while the cilia of the rest of the stomodæum work in the opposite direction. This differentiation of the stomodæum is particularly conspicuous in the Hexatinian Peachia, in which there is a deep strongly muscular groove along the whole length of one side (the so-called ventral side) of the stomodæum (fig. 6, *Si*); and the walls of the groove project at the mouth-opening beyond the rest of the wall of the stomodæum so as to form a semicircular lip conspicuous from the exterior at one end of the long axis of the mouth.

The free edges of this groove are frequently united with each other, so that the groove is converted into a canal open into the general cavity of the body at the lower end of the stomodæum, and to the exterior at the mouth-opening. This junction of the lips of the groove seems to be simply a case of adhesion, as they may with very slight effort be separated without tearing the tissue. When the groove is thus converted into a canal there are obviously two openings into the body of the polyp, one through the general opening of the stomodæum, and the other through this highly differentiated siphonoglyphe. According to Hickson (loc. cit.) the cilia work in opposite directions in these two parts of the stomo-

[1] 'Proc. Royal Soc.,' 1883.

dæum, so that one may be regarded as a mouth and the other as an anus.

I have not been able to make out what causes the adhesion of the lips of the siphonoglyphe in Peachia (whether interlocking of cilia as in Lamellibranch gill or what), but of the adhesion there can be no doubt whatever.

This differentiation of the mouth and stomodæum of Actinozooid polyps has been known for some time. The Hertwigs,[1] in their brilliant paper on the Actinozoa, summarise the facts and point out that the elongated mouth when closed has a dumb-bell shaped form, the median portion being closed, and the two ends remaining open.

"Wenn die Wandungen des Schlundrohrs an einander legt sind und der Mund geschlossen ist, bleiben sie (the 'Schlundrinnen') geoffnet und wird demnach ihre Bedeutung wohl darin bestehen, dass durch sie fortwährend ein Wasserstrom in das innere des Körpers hinein getrieben wird" (p. 513).

In view of the hypothesis under consideration, viz. that the mouth and anus of the higher animals is derived from an elongated slit-like opening such as is found in the Actinozoa, these anatomical facts are of the highest interest.

Blastopore of Peripatus.—The history of the blastopore of Peripatus has been given up to a certain point in the last volume (1883) of this Journal.[2] The youngest embryo found was a spherical or slightly oval gastrula with a slightly elongated blastopore (fig. 1). In the subsequent growth the embryo becomes elongated along the long axis of the blastopore and the mesoblastic somites appear (fig. 2). The middle portion of the lips of the blastopore then come together (fig. 3), and in the next stage (fig. 4) there are two openings into the mesenteron, an anterior and a posterior. Meanwhile, the primitive streak (connected with the formation of the meso-

[1] "Die Actinien," 'Jena Zeitschrift,' vol. xiii, p. 513.

[2] The species of Peripatus which Dr. v. Kennel is working at is different from that described in Balfour's memoir. Dr. v. Kennel does not mention this somewhat pertinent fact. Perhaps he was not aware of it; but if he was, I find it difficult to understand the positive nature of his criticism.

blast), which was present at the hind end of the blastopore in the earliest stage (fig. 1), has become marked with a groove (fig. 4). In the paper referred to, the question—Do these two openings become the mouth and anus of the adult?—was left open. I am now in a position to state that they do become the mouth and anus of an embryo of an age equal to the oldest stage described by Moseley[1] in his original paper, so that I think there can be no doubt that they do become the mouth and anus of the adult.

Thus, then, we have two undoubted facts:

1. That the mouth of the Actinozoa is differentiated into one portion for the exit and another for the entrance of matter, and that this differentiation is carried so far as to give rise to two separate openings (Peachia).

2. In the development of Peripatus capensis the single opening of the gastrula elongates, then divides into two parts, an anterior part which becomes the mouth, and a posterior which becomes the anus of the adult.

The argument may here be briefly summarised:

1. The blastopore of Annelida, Arthropoda, Mollusca, and the mouth of Cœlenterata are homologous because (*a*) of the development (*b*) of the anatomical relations in each case.

2. The structure of the mouth of Actinia and the position of the mouth and anus within the primitive nerve-ring, which is supposed to be homologous with the circumoral nervous diffusion of Actinia, obviously suggests the derivation of the mouth and anus from a single opening like the mouth of Actinia by the completion of the fusion which is there beginning.

3. The blastopore of Peripatus, which by hypothesis is homologous with the Cœlenterate mouth and with other blastopores, actually passes through the Actinia phase.

Is this development primitive? If it is primitive, then as the mouth and anus of Peripatus are homologous with those of Annelids, my point is gained and we shall have to take the second alternative (p. 52), and suppose that the peculiar

[1] 'Phil. Trans.,' 1874.

behaviour of the blastopore in other cases is due to larval specialisation.

The structure and distribution of Peripatus all point to its being an extremely primitive type. We should, therefore, a priori, expect to find that its development showed primitive features.

In the second part of this paper I shall attempt to show that the very variable behaviour of the blastopore is explicable.

It is hardly necessary to point out that the stomodæum and proctodæum are, on the above hypothesis, structures of purely secondary importance, and that I am in agreement with Balfour's suggestion that the stomodæum and proctodæum are not in all cases completely homologous. He says ('Comp. Emb.,' vol. ii, pp. 285, 286), "As a rule an oral and anal section of the alimentary tract—the stomodæum and proctodæum—are derived from the epiblast; but the limits of both these sections are so variable, sometimes even in closely allied forms, that it is difficult to avoid the conclusion that there is a border land between the epiblast and hypoblast, which appears by its development to belong in some forms to the epiblast and in some to the hypoblast." In other words, the development of certain parts of the alimentary canal may be so much delayed that they appear to arise from the epiblast.

This view is of special interest in considering the structures classed together as primitive streaks. As is well known, these structures are generally regarded as rudimentary parts of the blastopore (Balfour, Rauber). I would go further and suggest that it is an attempted development of that portion of the alimentary canal of the original ancestor which gave off the cœlomic pouches; that the portion which is not wanted in the development of simple larva of living animals is delayed, and consequently modified. I shall discuss this question at greater length in the second part of this paper.

I may conclude this part of my paper by describing briefly the ideal ancestor of the Cœlenterata and Triploblastic groups now under consideration, so far as the nervous system and mouth is concerned.

The Triploblastica and the Actinozoa are descended from a common two-layered bilateral ancestor which possessed an enlarged oral surface, an elongated mouth opening which by the adhesion of its middle portion was functionally divided into two openings, one at each end of the long axis of the mouth. The nervous system was generally distributed on the ectoderm all over the body, but was probably, as in living Actinozoa, especially concentrated on the oral surface. This type has persisted with certain modifications in Actinozoa, but in Peripatus and the other triploblastic forms under discussion the primitive mouth has completely divided, the body has elongated, and the nervous system has become especially aggregated in a ring (as in Medusæ) round the mouth and anus.

On the Origin of Metameric Segmentation.

It has for some time been recognised that the body cavity or cœlom of the Triploblastica has been derived from diverticula of the archenteron. Such diverticula have been known for some time in the Echinodermata, Sagitta, Brachiopoda, Balanoglossus, Amphioxus.

The development of the body cavity in Annelida, Arthropoda, Vertebrata, and other cœlomate forms without diverticula has been supposed to be an embryonic abbreviation of this primitive process. I may quote the following passages from Balfour on this head.

"The formation of hollow outgrowths of the archenteron, the cavities of which give rise to the body cavity, can only be explained on the supposition that the body cavity of the types in which such outgrowths occur is derived from diverticula cut off from the alimentary tract. The lining epithelium of the diverticula, the peritoneal epithelium, is clearly part of the primitive hypoblast, and this part of the mesoblast is clearly hypoblastic in origin. . . . There can be but little doubt that the mode of origin of the mesoblast in many Vertebrata, as two solid plates split off from the hypoblast, in which a cavity is secondarily developed, is an abbreviation of the process observable in Amphioxus; but this process approaches in some forms of Vertebrata to the ingrowth of the mesoblast from the lips of the blastopore.

"It is therefore highly probable that the paired ingrowths of the mesoblast from the lips of the blastopore may have been in the first instance derived from a pair of archenteric diverticula. This process of formation of the mesoblast is (as may be seen by reference to the summary (pp. 291, 292), the most frequent, including as it does the Chætopoda, the Mollusca, the Arthropoda," &c. ('Comp. Emb.,' vol. ii, pp. 293, 294).

It has been supposed until quite recently that only one pair of diverticula are developed (except in the Echinoderms and Balanoglossus). But Hatschek has shown that in Amphioxus, a very primitive and isolated animal, a series of diverticula are formed, each diverticulum giving rise to a mesoblastic somite, or, to put it in another way, that the lateral walls of the archenteron become folded before the region of the archenteron which they limit become separate from the central part of the archenteron. Amphioxus is the only segmented animal in which the body cavity is known to arise directly from archenteric pouches; development of the cœlom in other segmented animals being regarded as an abbreviation of a similar process. Now, however, that we know that the body cavity of Amphioxus is developed from a series of archenteric pouches, it seems to me that we are justified in concluding on similar grounds that the abbreviated development in other segmented forms is derived from a similar process.[1]

So that the difference between a segmented and an unsegmented animal consists in this, that in the former the archenteric walls become more folded than in the latter and give rise to a greater number of pouches, each of which becomes a mesoblastic somite. This is exactly the difference between a Hydra and a Medusa.

The similarity between the diploblastic Amphioxus embryo with a pouched gut (pouches giving rise to the mesoblastic somites) and an Actinozooid polyp or medusa suggests

[1] This has been already pointed out by Hubrecht; see Hubrecht, "On the Ancestral Form of the Chordata," this Journal, 1883.

very forcibly the hypothesis that the mesoblastic somites of segmented animals are derived from a diploblastic Cœlenterate-like ancestor with folded gut walls, the folding having arisen as a result of the necessity for an increase in the extent of the vegetative surfaces in a rapidly enlarging animal.

I would venture, therefore, to suggest that Medusæ, Actinozoa and segmented animals are all derived from a common diploblastic ancestor, the Gastræa; that as this Gastræa increased in size it became necessary that some arrangement should arise by which a proper circulation of the nutritive matter to all parts of the body should be effected. For this purpose the gut wall became folded in such a way as to give rise to the radial and circular canals of Medusæ; to the mesenterial chambers (communicating peripherally by mesenterial stomata) of Actinozoa, and to the pouched diploblastic form from which segmented animals have arisen (I do not mean to assert that the segmented animals are the only animals which have arisen from a diploblastic animal with a pouched gut; vide below p. 60).

In a segmented animal the mesoblast is the first part of the body to show segmentation. The rest of the segmentation is moulded on the segmentation of the mesoblast. That is to say, the segmented organs, primitively at any rate, correspond in their segmentation with the somites. For each somite there is the nephridium, nerve ganglion, &c.

Supposing there is anything in the hypothesis I am putting forward, viz. that the somites of segmented animals are derived from gut pouches, which are homologous with the alimentary pouches of Cœlenterata, then it ought to be possible to explain on the same hypothesis the similar repetition of other organs.

In a segmented animal the following organs usually show the same repetition as the mesoblastic somites; the external appendages, the nephrida, the muscular system and the nervous system.

In Cœlenterata, both in Medusæ and Actinozoa—

(1) The tentacles correspond as a rule to the radial canals or to the mesenterial pouches;

(2) In Medusæ there are a number of pores leading from the circular canal to the exterior, placed on the oral side of the insertion of a radial tentacle, i.e. opposite a radial canal; in Actinozoa there are a number of openings in the body wall, putting the pouches in communication with the exterior (for function and possible origin of these pores vide below, p. 62).

(3) In Medusæ the circular striated muscles of the subumbrella are interrupted by the radial canals (Hertwig) an so broken up into a number of segments.

(4) In Medusæ there are sense organs which may be in connection with special nervous aggregations (Acraspeda) at the periphery of each radius.

In segmented animals—

(1) When segmented appendages are present (Arthropoda, Polychæta) they are simply processes of the body wall containing prolongations of the body cavity (Peripatus, embryonic Arthropoda).

(2) The nephridia are essentially pores leading from the body cavity to the exterior on the neural side at the base of the appendage.

(3) The muscular system is sometimes broken up into bands corresponding to the segments.

(4) The nervous system sometimes presents swellings, one for each somite.

I further venture to suggest that the greater number of the Triploblastica have arisen from diploblastic animals with a pouched gut; that in some of these, in consequence of the form taken by the body (elongation) and the consequent necessity for jointing and the persistence and greater development of the paired appendages, the body has become moulded, so to speak on this primitive gut pouching, which has therefore left its trace in the "segmentation"; that in unsegmented Triploblastica, in consequence of the action of causes of an opposite nature to those just mentioned, the pouches, after becoming separated from the gut, have become completely continuous with one another and left no traces. As a known instance of the latter process I may mention Echiurus

(Hatschek); in this animal (in the adult) most of the nephridia have been lost, the three pairs which persist (two pairs of brown tubes and anal vesicles) being enlarged and modified; the gangliation of the ventral cord is lost and there are no traces of the somites.

To sum up in a few words:—The Cœlenterata differ from segmented animals only in the fact that the alimentary or archenteric pouches (mesoblastic somites) and the alimentary canal do not become separate; and connected with this absence of a distinct cœlom is the low state of differentiation of such cœlomic structures as the excretory organs and the absence of a separate vascular system.

On the Origin of the Excretory Organs.

This part of my subject is so closely connected with the preceding that it is difficult to separate the two.

I have already referred to the Hertwigs' observations[1] on the marginal pores of Medusæ and the cinclides of Actinozoa.

Metschnikoff was, I believe, the first to observe these marginal pores in Medusæ, and he regarded them as excretory; in this view the Hertwigs concur.

There is, then, this common feature in the anatomy of the Medusæ and Actinozoa; they both possess peripheral pores, putting the alimentary pouches in communication with the exterior.

In the Actinozoa they seem to have an irregular distribution as tentacular pores and cinclides (vide Hertwig). In the Medusæ, however, they have a definite position, one pore for each radial canal.

It seems an obvious suggestion that in the less specialised ancestors of Medusæ and Actinozoa these pores were distributed more or less irregularly as in the Actinozoa: that their position was determined by the habits of life and form of the animal.

[1] Vide Hertwig 'Organismus der Medusen,' p. 39, and Hertwig, 'Die Actinien.'

It is worth while trying to picture how such pores may have arisen. In the supposed ancestor the two layers of the body wall were in more or less close apposition. The animal had no vascular system, and only one more or less differentiated opening, the primitive mouth. It would obviously be convenient that the excretory products should pass out as near as possible to the point where they were formed, or that there should be some arrangement of ducts by which they could be carried to the mouth opening. The latter arrangement does not appear ever to have been developed in the Cœlenterata, while the former arrangement is present, if not in all, still in a great number of Medusæ and Actinozoa. My knowledge of the physiology of these low animals is not sufficient to enable me to offer any hypothesis of how the pores arose. But I may suggest that in the first instance the endoderm cells were of one kind only, whose function was to eat (in an amœboid manner) the food swept into the body cavity through the mouth opening, and to prepare soluble nutritive juices which passed to the ectoderm. The excretion of nitrogenous waste products must have been carried on by all the cells of the body, inasmuch as there is no circulatory system. The immediate undigestible remains or solid excreta from the endoderm cells would be cast into the alimentary cavity. Originally the latter must have been swept to the mouth and so got rid of. As the animal enlarged in size, and no well-developed canal apparatus appeared by which these solid waste products of the alimentary cavity would be directly carried to the mouth opening, some of the endoderm cells at the periphery of the animal became specially modified to eat these products, and pass them through or between the ectoderm cells to the exterior. So a close connection became established between the cells of the ectoderm and the endoderm, which eventually led to the establishment of a pore, the excretory pores. For an example of this kind of excretion through the ectoderm, I may refer to Eisig's [1] observations on

[1] "Die Segmentalorgane d. Capitelliden," 'Mitth. a. d. Zool. Stat. z. Neapel,' vol. i.

the Capitellidæ, in which the excretory organs end blindly against the ectoderm; their products, therefore, must pass to the exterior in some such way as I have suggested. If my suggestion be correct, it follows that the excretory organs were in their origin not specially organs for the excretion of nitrogenous waste products (each cell of the body being in close relation to the exterior did this itself) but for the riddance of the undigested and solid excretory products; and also that the excretory process was in its origin an intra-cellular process, i. e. temporary passages (amœba) were formed in the cells, through which the solid products passed to the exterior. This latter deduction is supported by the fact that in the higher animals the first formed excretory organs of the larva (Hatschek, Polygordius; Caldwell, Phoronis) have the form of delicate ducts attached to and opening through the ectoderm and ending in the body cavity, each in a simple cell; i. e. they are blind internally, and the excretory products in the body cavity must pass through the cell to get to the exterior.

Whatever view may be held as to the origin of the pores, the fact of their existence in the Diploblastica is undisputable.

At first irregularly arranged (a condition retained in Actinozoa, but more markedly in Sponges), they soon acquired a regular arrangement (Medusæ), and on the differentiation of the alimentary cavity into a digestive part (gut proper), and a circulatory and excretory part (cœlom), they remained in connection with the cœlom, which latter became again differentiated into parts purely excretory and connected with the pores (nephridia), and into the general vascular space for the circulation of the nutritive fluids passed into it from the endoderm cells.

Turning to the development of the excretory organs of the higher animals, we find that in the Vertebrata they arise as special parts [1] (not mere outgrowths) of the cœlom, and I have no doubt that this will be soon shown to be the case for the development of the Invertebrate excretory organs.

[1] Sedgwick, "Development of Kidney, &c.," 'Quart. Journ. of Mic. Sci.,' vol. xx, 1880.

Here, however, an apparent difficulty presents itself. In the Vertebrata the excretory organs (which probably were primitively segmental [1]) open not to the exterior direct, but into a longitudinal canal which opens behind into the alimentary canal; while in the Invertebrata each of them opens direct to the exterior.

As an explanation of this difficulty I suggest that in the Vertebrate ancestors the primitive alimentary cavity acquired a well arranged system of ducts, by which the peripheral excretory matters were carried to the part of the alimentary canal near the hind end of the primitive mouth (future anus), that in consequence the excretory pores were not wanted, and were either never developed or if developed lost. As confirmatory evidence I may refer (1) to the circular canal of the Medusæ, which might easily be conceived transformed into the Vertebrate segmental duct, the excretory organs themselves being developed from the outer part of the radial canals; (2) to the method of development of the anterior and least modified part of the Vertebrate excretory organ. In the osseous fishes and Amphibia the segmental or pronephric duct arises as a groove of the body cavity, and is therefore a direct product of the archenteric endoderm. In most Vertebrates the development of the segmental duct is much modified; but I pointed out some years ago that we can only get an intelligible explanation of the connection between the excretory tubules and the duct of the kidney by supposing that they originally developed in continuity, both as specialised parts of the body cavity, and that this method of development is repeated in the case of the anterior part of the kidney of Ichthyopsida, and in a more modified manner in the Amniota.

Turning to the Invertebrata, we find that the development is not direct from the cœlom, but from solid masses of cells [2]

[1] Elasmobranchs. For discussion of this question, vide Sedgwick, "Early Development of Wolffian Duct," 'Quart. Journ. of Mic. Sci.,' vol. xxi, 1881.

[2] Very various accounts are given of the origin of the Invertebrate excretory organs. I reserve a critical examination of these facts until I have worked out the development of the nephridia of Peripatus.

derived from its walls. This may reasonably be explained in the same way as I have attempted to explain in my paper quoted above, the development of the hinder part of the Amphibian kidney (modified larval development).

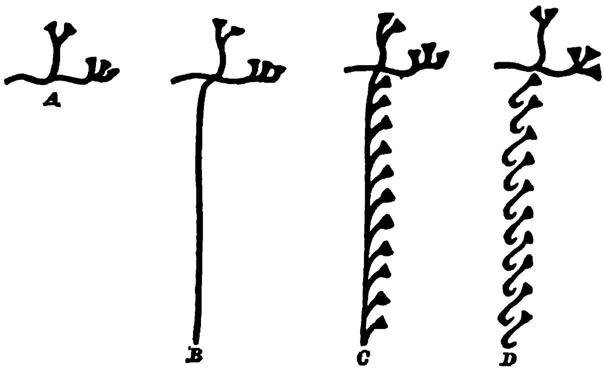


FIG. 1.—Diagram illustrating the development of the excretory system of Polygordius (from Balfour, after Hatschek).

The development of the excretory organs in Polygordius (woodcut, fig. 1) as described by Hatschek, is explicable on my hypothesis and so is confirmatory. The temporary longitudinal canal, which at first connects all the organs, is obviously a rudiment of the longitudinal duct found in the Vertebrata. The presence of this duct indicates that in the diploblastic ancestor of Polygordius, a system of canals was present in the cœlom together with the excretory pores.

ON THE ORIGIN OF TRACHEÆ AND GILL SLITS.

The view that tracheæ are derived from the cutaneous glands of a worm-like ancestor with a well developed middle layer is beset with so many physiological difficulties that I venture to suggest the following hypothesis, which agrees equally well with what we know of the development of tracheæ.

Tracheæ had their origin, like the organs so far discussed, in the diploblastic ancestor. In this ancestor they had the form of simple ectodermic pits developed for the purpose of aerating those organs, whose position prevented their getting a sufficient supply of oxygen from the external medium or from the water circulating in the alimentary cavity. It must be remembered that there was no vascular system in this ancestor, and that therefore the living protoplasm of all parts of the body had to obtain its oxygen directly from the external medium. This method of aeration has persisted at the present day in certain Medusæ (sub-genital pits), in the Tracheate Arthropoda, and has left its trace in the Vertebrata in the canal of the central nervous system.

On this hypothesis the complicated distribution of tracheæ receives a physiologically satisfactory phylogenetic explanation.

The tracheæ were at first simple pits of ectoderm in a diploblastic animal, and they gradually became more complicated and branched as the other organs also became more complicated and folded.

The development of tracheæ fits in perfectly well with this view.

The tracheal respiration is then a primitive method of respiration, which has persisted in but few of the Triploblastica. It had its origin at a time before the vascular system was developed, and its essence consists in the fact that the living protoplasm takes its oxygen direct from the external medium. On this hypothesis the central canal of the central nervous system was a respiratory organ in a diploblastic Vertebrate ancestor without a well developed vascular system.

As soon as the vascular system became well developed, and the vascular fluid capable of carrying oxygen, the respiratory organs became localised. A special localisation of tracheæ is found in the pulmonary sacs of the Scorpion. In other animals external appendages have arisen. But in Vertebrata, Balanoglossus, and Ascidians, the circulation of water over the surface of the endoderm has been more developed. In the Diploblastic ancestor respiration was, as I have stated, partly effected by water circulating in the alimentary cavity. It entered by one end of the mouth and passed out partly through the other end, and partly through the excretory pores of the alimentary pouches. Some of these alimentary pouches became, on the development of a vascular system, specialised as respiratory organs and retained their communication both with the exterior and with the alimentary cavity.

Thus gill slits are serially homologous with nephridia. This view of their origin is entirely supported by their development from pouches of the hypoblast of Vertebrate embryos, and by the fact that the kidney system in Vertebrata does not overlap them, but begins immediately behind them. A difficulty to this view lies in the fact that the cœlom does overlap the gill slits; but I think this difficulty is not a serious one when we remember that the cœlom being originally a vascular space had to extend in the region of gill slits as elsewhere, and that this extension might easily have proceeded either from the mesoblastic somite next behind the last gill pouch, or from a compression of the body in this region so that many somites (probably after separation from the archenteron) extended into the region of the gill slits.

Summary.

The hypothesis suggested in the preceding pages are all based upon the gastræa theory, developed by Lankester and Hæckel. I take the gastræa as my starting point and do not inquire how the gastræa itself arose. I first (p. 8 to p. 17) by following the gastræa theory to its logical conclusion—and there seems recently to have been a disinclination on the part of some morphologists to do this—attempt to show that the gastræa mouth is not only homologous with the Cœlenterate mouth, but that the blastopore of the embryos of the Triploblastica is homologous with the gastræa mouth, and therefore homologous with the Cœlenterate mouth; and, finally, that if these necessary deductions from the gastræa theory are correct, and it should be noticed that the gastræa theory itself stands or falls with them—it necessarily follows (from the consideration of the Peripatus embryo) that the mouth and anus of the Triploblastica are derived from the gastræa mouth, i. e. Cœlenterate mouth. I have pointed out that the blastopore in becoming the larval mouth must have become highly specialised and unable in most cases to repeat its ancestral history in the larval development, and that the behaviour of the blastopore becomes much more intelligible, though, I admit, not entirely so.[1] The remainder of my hypotheses are simply following the lines of the recent speculations on the origin of the nervous and muscular tissue. My speculations, like these, are based (1) on facts of Cœlenterate anatomy which have been mainly brought to light by the magnificent work of the Hertwigs. (2) On facts of embryonic development which have been for the most part long known, but have recently been added to in an important manner by Hatschek's work on Amphioxus and Balfour's discovery of the embryo of Peripatus capensis. The object of my speculation has been to extend Balfour's theory of the Triploblastic nervous system to the remaining systems of organs; in other words, I have attempted to show that the majority of the Triploblastica (I confine myself to the Annelida, Arthropoda Mollusca, Vertebrata and certain small groups, e. g. Balanoglossus, Sagitta, Brachiopoda) are built upon a common plan; and that that plan is revealed by a careful examination of the anatomy of Cœlenterata: that all the most important organ systems of these Triploblastica are found in a rudimentary condition in the Cœlenterata; and that all the Triploblastica referred to must be traced back to a common diploblastic ancestor common to them and the Cœlenterata.

[1] I shall return to a consideration of the behaviour of the blastopore in the second part of this paper.

PART II.

Application of the above Hypotheses to the Vertebrata, Annelida, Arthropoda, Mollusca, and certain smaller groups.

Fig. 7 represents a diagram of the ideal ancestor of all the above-mentioned Triploblastica. It closely resembles the common ancestor of the Cœlenterata but may be supposed a little more advanced in specialisation. For instance, the peripheral excretory pores (*o*) have a regular arrangement. This animal is supposed to have a bilateral symmetry shown in the gut pouches and in the excretory pores. It is supposed to have an elongated mouth partly differentiated into two parts, and the nervous system is generally diffused over the oral surface (which will henceforth be called the neural surface) with a tendency to specialisation into a narrow tract.

This ideal ancestor soon gave rise to two stocks, the first differences between which may be supposed to depend on the shape of the body.

In the one stock the mouth and anus (which soon became separated) remain on the neural surface, a præoral lobe was developed on the abneural surface of the body (fig. 12); this præoral lobe being carried first in movement became specially sensitive and the nervous system largely developed.

This stock is the **Invertebrate stock.** The præoral part of the nervous ring in consequence of the shape the body has taken becomes enlarged and sense organs largely developed in connection with it. The hinder præanal parts of the nervous ring have more or less approximated to each other, and are connected by commissures and become swollen at intervals where many nerves pass out to the locomotive organs (appendages). The postanal part of the ring becomes weak and often disappears, never having more than a commissural function (absence of nerve-cells in postanal connection of lateral nerve trunks of Peripatus, vide Balfour on Peripatus capensis).

With regard to the endodermal organs the alimentary pouches have lost not only their connection with the alimentary cavity and now constitute mesoblastic somites (fig. 8), but have also lost their peripheral connection with each other. The excretory pores persist and the part of the somites near the pore becomes developed into the nephridia.

In the other stock the body assumed a different shape, in consequence of which the mouth and anus became terminal (vide fig. 13, ideal). A projection overhanging the mouth then appeared on the neural surface and gave rise to a neural præoral lobe (fig. 14.) The præoral and postanal part (N^1 and N^2) of the nervous ring soon became inconspicuous and vanished. (It must be remembered that the nervous system of this stage of evolution was little, if at all, more developed than that of living Actinozoa.) This is the **stock** of the **Vertebrata** and **Balanoglossus.** The part of the primitive ring immediately behind the mouth is the most important in this stock; it is placed at the anterior end of the body, and therefore enlarges and develops sense organs. (Fig. 14.)

With regard to the endodermal organs the pouches have become differentiated into two kinds:

(1) Anteriorly a certain number retain their communication with the exterior and with the gut. (Fig. 10.)

(2) The majority, however, lose their connection with the gut and with the exterior, but remain connected by the peripheral canal, which behind retains (by means of a pouch?) its communication with the gut.

(3) A posterior pouch loses its connection with the gut and with the longitudinal canal, and gives rise to an abdominal pore.

The first group of pouches become the gill slits, the second become the cœlom, while part of each of them become differentiated into nephridia which opens into the longitudinal canal (pronephric or segmental duct). The last pair of pouches gives rise to a part of the cœlom and retains ts connection with the exterior as an abdominal pore.

The further evolution of the Invertebrate Stock.—Paired processes of the body wall (fig. 10), into which the cavities of the somites were continued are present (generally homologous with tentacles of Cœlenterata which correspond with the mesenterial chambers or radial canals). These become specially locomotive, and consequently muscular; hence the swellings (ganglia) on the nerve cords, each swelling corresponding to appendages, i. e. to a somite.

The septa between the pouches have more or less broken down, so that the cœlomic spaces become connected; the dorsal or ventral mesenteries, both or one of them, likewise break down.

Sometimes the appendages vanish (Gephyrea, Mollusca), the ganglionic swellings then disappear, and the only trace in the adult of the embryonic segmentation is seen in the nephridia. Many of these must, however, have vanished (according to Hatschek's account of development of Echiurus), and two or three or four pairs have become enlarged and alone persisted. It is interesting to notice the differentiation of the persisting nephridia in the Gephyrea into the brown tubes, which act as excretory organs and generative ducts, and the anal vesicles. This differentiation of the nephridia of different parts of the body is carried, as we shall see, much higher in the Vertebrata. In the Mollusca the disappearance of the somites has gone even further than in the Gephyrea, and the cœlom has become much modified. In Nautilus, however, a trace of the original segmentation persists in the nephridia and vascular system.

The development of Sagitta indicates that it is derived from an ancestor with three pairs of pouches, two of which retain their external pores (generative orifices). The Brachiopoda I at present leave out of special consideration.

Thus, the number of pouches (segments) in the Tripoblastica varies in different cases, just as do the alimentary diverticula of the Actinozoa.

The further evolution of the Vertebrate Stock.—The central nervous system which is almost entirely derived from that part of the primitive ring intervening between the mouth and anus, unites more or less completely across the middle line.

It and the superficial epiblast with which it is in connection become grooved; the groove becomes deepened and converted into a canal open close to the mouth in front and close to the anus behind (fig. 15).

The function[1] of this canal at this stage (the siphon stage) I have elsewhere discussed and ventured to suggest that it was in the main respiratory. (For the embryological counterpart of the siphon stage, see below, p. 75.)

It is important to notice that the nervous system of the Vertebrata becomes removed from the surface in quite a different way to that which obtains in the Invertebrata. In the latter it becomes removed from the surface by the ingrowth of mesoblastic tissue between it and the superficial layer in connection with which it arose. In the former, on the other hand, it never separates from the superficial epiblast from which it arises. The latter is involuted with the nervous mass and persists through life as the lining of the canal of the Vertebrate nervous system. This fact is of great importance in speculating on the origin of the Vertebrata, for it shows that the Vertebrate stock is a very primitive one, and must have separated from the Invertebrate stock before the nervous system of the latter separated from the epidermis.[2]

It will be observed that in consequence of the development of the præoral lobe (fig. 15 not marked enough), the mouth has become placed on the other side of the body, i. e. on the abneural side, and the neural canal has to bend towards this surface (the future ventral surface) in order to open into the mouth.

The water which was attracted by the ciliary movement

[1] For a discussion of the function of the canal at this stage, *vide* Sedgwick, "On the Original Function of the Canal of the Central Nervous System of Vertebrata," 'Proceedings of the Cambridge Philosophical Soc.,' vol. iv.

[2] This fact also holds for the cerebral ganglia of Peripatus; the invaginations of ectoderm become constricted off, and their cavities persist throughout life in the ventral protuberances of the brain.

divided at the anterior opening (fig. 15) into two streams, one of which passed through the mouth into the alimentary canal, while the other passed through the neural canal.

There was probably an olfactory sense organ developed from the epiblast close to the front end of the neural canal over which this water rushed.

The anterior convex wall of the neural canal now becomes bulged out forwards, and gives rise to a large anterior lobe, whose cavity opens behind into the neural canal, close to its opening into the mouth (fig. 16). This anterior lobe carries with it the olfactory epithelium, which, however, remains in connection with the mouth by grooves or canals. It becomes bi-lobed and transformed into the cerebral hemispheres of living Vertebrates.

The neural canal now closes both in front and behind, and assumes some other function than that of respiration. Behind the closing leaves no trace, while in front remains of the connection are seen at the present day in the infundibulum, and in the pituitary body.

It will be evident from the above hypothetical account of the origin of the Vertebrata, that I believe that the mouth and anus of the Vertebrata are homologous with the corresponding structures in the Invertebrate segmented animals. I have stated above, that I suppose that the blastopore of the Vertebrata is a specialised larval structure derived from the primitive mouth of a two-layered ancestor. It will be obvious also, that, according to my view, the position of this primitive mouth coincided with the middle line of the dorsal surface of the Vertebrate embryo, and that supposing it persisted in its primitive form in the embryo until the adult mouth and anus were formed, it would appear as a slit extending from the mouth anteriorly and ventrally round the front end of the head, along the whole surface of the medullary groove to the primitive streak round the hind end to the ventrally placed anus.

In the first part of this essay which deals with the blastopore, I have attempted to show that the mouth and anus of segmented Triploblastica are in all cases derived from a primitive single mouth; that this primitive mouth is represented in the embryo by the blastopore which should, if the phylogenetic development were repeated, give rise directly to the mouth and anus. I explained the fact that the blastopore so rarely does give rise to the mouth and anus by supposing that it became specialised as a larval[1] structure. My view is that in those animals in which it does not give rise to the mouth and anus, it functioned as the larval mouth while the animal was developing, and persisted until parts of the embryo were developed between it and the position of the mouth and anus of the adult, which parts had arisen in the phylogenetic history in the adult after the primitive mouth had completely divided into the mouth and anus. These parts never had been traversed by the original slit-like mouth, because they had appeared at a stage in evolution subsequent to the stage in which the mouth and anus were one. It cannot therefore be a matter of surprise if the blastopore does not elongate and bisect these later structures, which never had in the history of the animal been perforated by the blastopore. It is very difficult for me to express my meaning in clear language, and I am driven to take an instance to illustrate it. According to my view the cerebral hemispheres have appeared at a stage in the evolution of the Vertebrata long after the primitive mouth has become separated into the mouth and anus. The blastopore (primitive mouth), however, which has in some ancestral Vertebrate functioned for a considerable time in the larva as the only opening into the alimentary canal, persists and does not elongate to give rise to the mouth and anus which are not formed until after the cerebral hemispheres have appeared. It is now no longer possible, nor would it be advantageous if it could, that the specialised blastopore should elongate and give rise to the mouth and anus, the middle part closing up. The cerebral hemispheres have appeared, and they have never in the phylo-

[1] The larval stage, for which the mouth was specialised, has in the Vertebrata, as in many other animals, vanished; it has probably been included in the embryonic period, and rapidly hurried over.

genetic history been traversed by this slit. Consequently the only course open is that the mouth should be formed as a secondary perforation entirely independent of the blastopore.

From the nature of the case it is exceedingly difficult to bring forward any direct proofs derived from embryology in favour of this view. But I think it can be shown that there is reason to believe that the mouth and anus of the Vertebrata are placed in the line of the original blastopore. Amphioxus, so far as I understand its development, offers no support to my view, but the case is different with the Ascidians and the higher Vertebrata.

Weldon[1] has shown conclusively that the anus is formed within the area of the primitive streak, though after the disappearance of the latter structure. It is on all hands admitted that the primitive streak is a part of the original blastopore. I need, therefore, say nothing with regard to the anus.

The mouth, however, is a great difficulty. Dr. Dohrn has attempted to show that it is derived from a pair of gill slits. Now, without considering the embryological facts opposed to his view, which have been so ably pointed out by Balfour, I venture to suggest that it is exceedingly improbable that an animal should lose its mouth and develope a new one. It is surely, on a priori grounds, far more likely that it would change gradually the position of its mouth than that it should lose it and go through the labour of acquiring a new one, though that new one is supposed to be derived from preexisting structures.

Turning to the actual development, I may mention here two facts which appear to me of importance.

(1) In Ascidians, Kowalewsky[2] has shown that the mouth at a certain stage is dorsal (neural), and that the neural canal opens into it (woodcut, fig. 2, V). The neural canal, also, at a slightly earlier, if not contemporaneous stage, opened behind into the gut. We thus find the hypothetical siphon stage of the evolution of the neural canal actually repeated in the

[1] 'Quart. Journ. of Mic. Sci.,' 1883.

[2] Kowalewsky, 'Arch. f. Mic. Anatomie,' vol. vii, 1871.

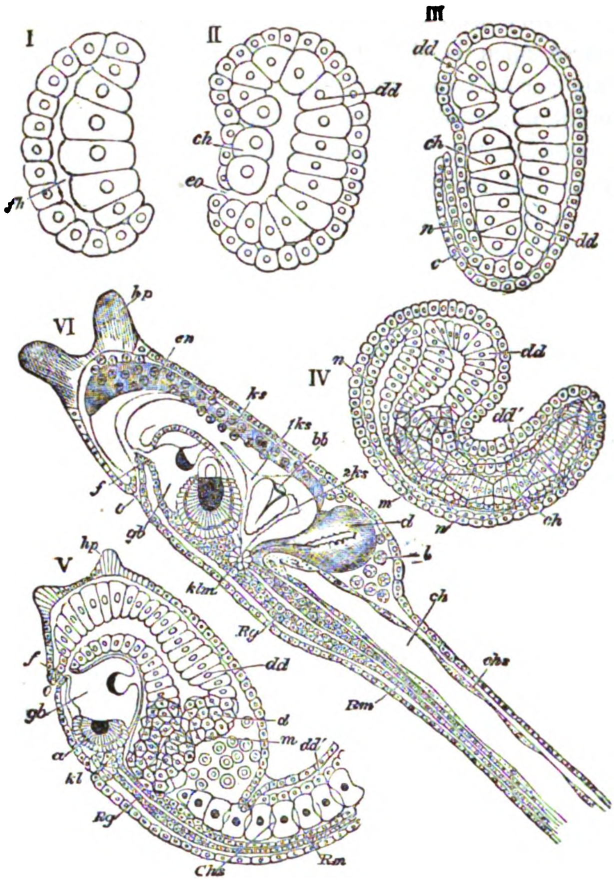


FIG. 2.—Various stages in the development of Phallusia mammillata (from Huxley; after Kowalewsky). I. Commencing gastrula. *fh.* Segmentation cavity. II. Late gastrula stage. *eo.* Blastopore. *ch.* Notochord. *dd.* Hypoblast. III. More advanced embryo. *n.* Neural tube. *e.* Epiblast. IV. Formation of neural tube completed. *dd'.* Hypoblast in tail. *m.* Muscles. V. Larva just hatched, the end of the tail is not represented. *a.* Eye. *gb.* Dilated extremity of neural tube, with otolith projecting into it. *Rg.* Anterior swelling of spinal division of neural tube. *f.* Anterior pore of neural tube. *Rm.* Posterior part of neural tube. *o.* Mouth. *chs.* Notochord. *kl.* Atrial invagination. *dd.* Branchial region of alimentary tract. *d.* Commencement of œsophagus and stomach. *dd'.* Hypoblast in tail. *m.* Muscles. *hp.* Papilla for attachment. VI. Body and anterior part of a two days' larva.

development of a living form. Salensky[1] long ago pointed this out. With a slight change in the shape of the anterior end of the body of the Ascidian larva in Kowalewsky's figure, the mouth would be removed from what we call the dorsal (neural) to what we call the ventral (abneural) surface. This would involve a flexure of the anterior end of the neural canal, and, I think, gives a clue to the phylogenetic meaning of the cranial flexure. The closure of the anterior pore of the neural canal is effected in such a way that it leaves a trace on the one hand as the infundibulum; on the other as the pituitary body. This homology has been often suggested. The persistence of the lower part of this pore, and its development from the epiblast of the buccal cavity, may be explained by supposing that the buccal end of the pore was glandular before the closure of the neural canal was effected. When this closure was effected, the buccal part remained in connection with the mouth as an excretory organ, a state of things persisting, according to Salensky, in Ascidians. It then acquired the new functions which it has at present, lost in the adult its connection with the mouth, and is known to us as the pituitary body. Meanwhile, some of the endoderm cells of the dorsal wall of the alimentary canal have become specially modified and separated from the rest as the notochord.

(2) In the Vertebrata the anterior end of the notochord is bent round, and becomes connected with the pituitary body at its extreme front end.[2] This condition of the anterior end of the notochord may be seen in the embryo before the pituitary involution is cut off from the ectoderm of the developing mouth—that is to say, the relation of the anterior end of the notochord to the ectoderm is similar to that of the hind end;

[1] Salensky, 'Zeitschrift f. Wiss. Zoologie,' vol. xxvii, p. 212; and 'Morphol. Jahrbuch.,' vol. iii, p. 600.

[2] The relation of the anterior end of the notochord to the pituitary body is somewhat complicated. For the knowledge of this fact I am indebted to Mr. Heape, who is at present engaged in investigating this very point. He informs me that the existence of the connection was known to the older embryologists (W. Müller).

behind it is closely connected with the front wall of the neurenteric canal; in front it is closely connected with the ectoderm of the developing buccal cavity.

At a still earlier stage, before the cranial flexure has appeared, the front end of the notochord is swollen, and runs into and is continuous with the front end of the medullary plate. This state of things I have myself observed at a stage before the medullary plate has begun to fold. Now, my view is that this connection of the notochord marks the site of the future mouth; that the site of the mouth—at first as in Ascidians—perforates the medullary plate, and is on the dorsal surface; that soon, however, this site bends round on to the ventral surface, and is eventually invaginated to form the buccal cavity and pituitary body. This hypothesis can easily be tested in the chick with the new Caldwell automatic microtome, but I regret that I have not hitherto found time to do so.

(Professor Hubrecht in his ingenious paper already quoted (this Journal, 1883), has instituted a comparison between the pituitary body and notochord of Vertebrates and the proboscis and proboscis sheath of Nemertines.)

The cerebral hemispheres appear relatively late in front of the notochord, and this fact fits in very well with the account of their origin which I have suggested. On this view Amphioxus has separated from the vertebrate stock before the appearances of the cerebral hemispheres.

The modification of the alimentary pouches, and the longitudinal canal connecting them, I have already alluded to. It only remains for me to point out that the cavities of the mesoblastic somites soon come to communicate ventrally both with each other and those of the opposite side; that the dorsal mesentery for the most part only persists, though the ventral mesentery remain in the region of the heart, liver, and behind in the region of the hind part of the body; that the nephridia become modified into groups, each with a special importance; the pronephros, or larval organ, is the first formed part of the kidney and atrophies in the adult; the hinder part differentiates into meso- and meta-nephros; the meso-nephros becomes connected with the male generative organs, and loses its excretory function, while the metanephros persists as the functional kidney. I have, however, fully discussed the evolution of the Vertebrate excretory system in my papers already quoted on their development, and need not refer further to it here, except to point out that there is every reason to believe that the nephridia were originally segmental, one for each somite, that this segmental arrangement is, with the specialisation of the kidney, soon lost as it is in other organs.

On the Structures known as Primitive Streaks.

I may conclude this paper by a short review of these structures.

(1) They are always connected with the formation of the mesoblast.

(2) They are never, so far as I know, found in free larvæ. They are confined to the embryonic phase of development, and are only found in animals which undergo a considerable part of their development in the egg; in other words, only in eggs well-stocked with food yolk, or in eggs which have lost the food yolk. On the other hand, a primitive streak is not universally present in such cases, e.g. Cephalopoda, Elasmobranchii, Amphibia, Crustacea.

(3) They are always median and unpaired in their origin, but may in later development become grooved and present traces of a bilateral structure.

(4) They are always caused by rapid proliferation of cells, apparently from the epiblast.

(5) Their position seems to vary in different animals.

In Vertebrata, when present, the primitive streak is placed mainly behind the blastopore (according to Strahl[1] not entirely so in Lacerta, but this is not quite clear from his figures).

In Peripatus it is placed behind the blastopore, and, when the blastopore has divided, behind the hinder division (fig. 4).

[1] 'Arch. f. Anat. u. Phys.,' 1882.

In other Arthropoda in which a primitive streak is present, its position with regard to the blastopore cannot be determined; because the blastopore is not present in those cases in which there is a primitive streak.

With regard to the two first cases the blastopore of the Vertebrata closes, and the anus is subsequently (very late) formed within the area of the primitive streak.

In Peripatus, however, the hinder division of the blastopore does not close but travels slowly back over the area occupied by the primitive streak to its position at the hind end of the body.

I may here mention a fact which I observed last summer in the newt (Triton cristatus). In this animal the blastopore appears not to close but to persist as the anus. This statement is based on surface views of a large number of embryos from the stage when the egg is round until hatching. In all these stages I never saw an embryo without an opening at the hind end of its body. I very much regret that I have not had time to confirm this observation by means of sections.

If true it is most interesting as being the only known case in which the blastopore of Vertebrata actually persists as the anus.

In the case of larvæ which leave the egg at an early stage of development, no primitive streak is developed, but the mesoblast partly grows in from the lips of the blastopore, and partly arises as mesenchyme.

In Amphioxus fourteen pairs of somites are derived as hypoblastic pouches, the remainder are formed from hypoblastic tissue, the exact behaviour of which is not explained by Hatschek.

In those Vertebrata with primitive streak, the anterior somites may be regarded as arising from hypoblastic mesoblast; but the greater part are formed from primitive streak mesoblast.

In Peripatus, the mesoblast arises behind the blastopore from the primitive streak, and grows forward as two bands, exactly as in worms; but it arises from a primitive streak.

I do not think any really satisfactory explanation can be offered at present of these facts. I venture, however, to suggest the following as an attempt at an explanation.

In many living Triploblastica the embryo leaves the egg at a very early stage as a larva; at a stage in which it is little more than a gastrula. Inasmuch as the parent of this ancestor has differentiated nephridia and muscles, &c., it is easily conceivable that the larva should precociously acquire as much of these organs as it requires. Hence mesenchyme. This larva is a small animal, and does not require a pouched gut; its hypoblast becomes specialised for digestion; now it would obviously hamper these exceedingly active larvæ if the gut repeated the phylogeny; at any rate, it is easily conceivable that it would be more advantageous if it were possible that the digestive cells should not have to undergo active developmental changes. Hence the mesoblast has to be formed in another way. The methods in which it is formed are, as is well known, various; it nearly always, however, originates at the lips of the blastopore, as the result of the proliferation of a cell, or cells, which do nothing else but divide and give origin to the mesoblastic bands. This, as I have suggested above, may be looked upon as a modified development of that of the ancestral archenteron, which became pouched, and gave rise to somites (secondary invagination).

In those animals in which this larval phase has become merged in the embryonic development, this process is continued; but the area from which the major part of the mesoblast arises, i. e. from which the secondary invagination takes place, is larger. This may obviously be explained as being due to the fact that, the development being protected, it is not important that the amount of growing tissue present at any given moment should be as small as possible, in order not to hamper the larva.

On this view Amphioxus presents a most surprisingly primitive development, so far as its somites are concerned.

I need hardly point out that the prevailing order of development, from before backwards, is just what would, a priori, be expected. The larva, being a free swimming animal, requires sense organs; it therefore develops its anterior part first and the organs belonging to this region of the body.

EXPLANATION OF PLATES II & III,

Illustrating Mr. Sedgwick's Paper on the "Origin of Metameric Segmentation."

Complete List of Reference Letters.

A. Anus. *a.* Anterior end of young embryo. *A. P.* Abdominal pore. *B.* Body-wall. *C. H.* Cerebral hemisphere. *C.* Longitudinal canal connecting pouches of archenteron. *E.* Ectoderm. *G.* Gill pouch. *H.* Heart. *K.* Nephridium. *K. D.* Longitudinal duct of Nephridia (segmental duct). *M.* Mouth. *M. A.* Coalesced part of primitive mouth. *ME.* Mesenteron. *me.* Edge of mesenteries. *M. S.* Mesoblastic Somites. *N.* Nervous system between mouth and anus. N^1. Præoral part of nervous system. N^2. Postanal part of nervous system. *N. C.* Neural canal. *Ne.* Posterior opening of neural canal. *O.* External openings of Nephridia. *P.* Pouches of archenteron. *P.* Præoral lobe. *Py.* Anterior opening of neural canal. *Si.* Siphonoglyphe. *Si'.* Upper end of siphonoglyphe projecting beyond general edges of lips. *St.* Wall of stomodæum.

Figs. 1—5.—Five young embryos of Peripatus capensis, ventral view. From drawings by Miss Balfour. *a.* Denotes the anterior extremity.

Fig. 1.—Youngest embryo, with slightly elongated blastopore.

Fig. 2.—Embryo, with three somites and elongated blastopore.

Fig. 3.—Embryo, with five somites. The blastopore is closing in its middle portion.

Fig. 4.—The blastopore has completely closed in its middle portion and given rise to two openings, the future mouth and anus. The primitive streak is deeply grooved.

Fig. 5.—Embryo, with about thirteen somites; flexure of hind part of body commenced. The remains of the original blastopore are present, as the mouth placed between the second pair of somites, and the anus placed on the concavity of the commencing flexure of the hind part of the body.

Fig. 6.—Stomodæum of Peachia, laid open so as to show the siphonoglyphe. This figure was very kindly drawn for me by Mr. W. F. R. Weldon. *T.* Tentacles. *St.* Wall of stomodæum. *Si.* Siphonoglyphe. *Si'.* Upper end of siphonoglyphe, projecting beyond the general edges of the lips. *B.* Body-wall. *me.* Edge of mesenteries.

FIG. 7.—Diagram of ideal ancestor of segmented animals, viewed as a transparent object from the ventral surface. *A*. Central part of archenteron. *P*. Pouches of archenteron (four represented on either side). *C*. Longitudinal canal connecting pouches. *O*. Excretory pores. *N*. Nervous ring. *M. A*. Dumb-bell shaped mouth. Ectoderm.

FIG. 8.—Diagram showing Invertebrate arrangement. Archenteric pouches separate from central part of archenteron (now called mesenteron). *E*. Ectoderm. *M.E*. Mesenteron. *M. S*. Mesoblastic somites. *K*. Nephridia. *O*. External openings of Nephridia. *M*. Mouth. *A*. Anus. *M. A*. Coalesced medium part of primitive mouth. *N*. Central nervous system; dumb-bell shaped like that of Peripatus. Wall of mesenteron, yellow. Mesoblastic somites, blue. Nephridia, red.

FIG. 9.—Diagram of Vertebrate arrangement from neural (dorsal, i.e. ventral of Invertebrata). Excretory pores are not developed, except behind, *A. P.*; and in front, *G*. Colours and letters as in Fig. 8, except *G*, gill pouch. *K. D*. Longitudinal duct of Nephridia, or segmental duct, opening behind into mesenteron. *A. P*. Pore retaining Invertebrate arrangement= abdominal pore. Mouth, anus, and nervous system not shown.

FIG. 10.—Diagrammatic transverse section through Invertebrate. Colours as before. *M. S*. Somite. *M. E*. Mesenteron. *N*. Nervous system. *K*. Nephridia.

FIG. 11.—Diagrammatic transverse section through Vertebrate. Colours as before. *N. C*. Neural canal. *M. E*. Mesenteron. *K. D*. Segmental duct. *K*. Segmental tube (nephridium). *M. S*. Somite.

FIG. 12.—Diagram of longitudinal vertical section of Invertebrate. Vascular system, red. *P*. Præoral lobe (hæmal). *H*. Heart. *N*. Nervous system. N^1. Præoral nervous system. N^2. Postanal ditto. *M. E*. Mesenteron. *M*. Mouth. *A*. Anus.

FIG. 13.—Diagram of ideal intermediate type, with terminal mouth and anus. Letters and colours as in Fig. 12.

FIG. 14.—Diagram of arrangement of Balanoglossus, with neural præoral lobe and without præoral and postanal nervous system.

FIG. 15.—Diagram of arrangement of embryo Ascidians and Vertebrata. Nervous system folded in. (Siphon stage.) *Py*. Anterior opening of neural canal (site of the pituitary body). *Ne*. Posterior ditto. *N. C*. Neural canal.

FIG. 16.—Diagram of Vertebrate arrangement. *C. H*. Cerebral lobe.

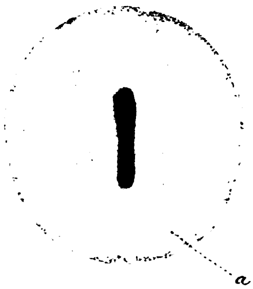


Fig. 1.

Fig. 2.

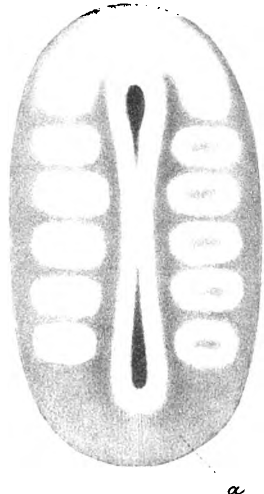


Fig. 3.

Fig. 4.

Fig. 5.

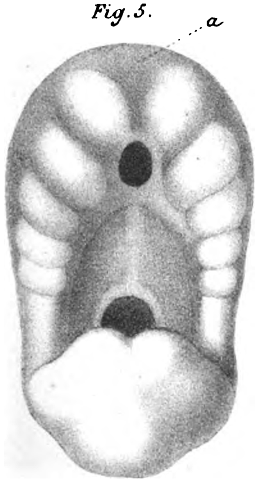
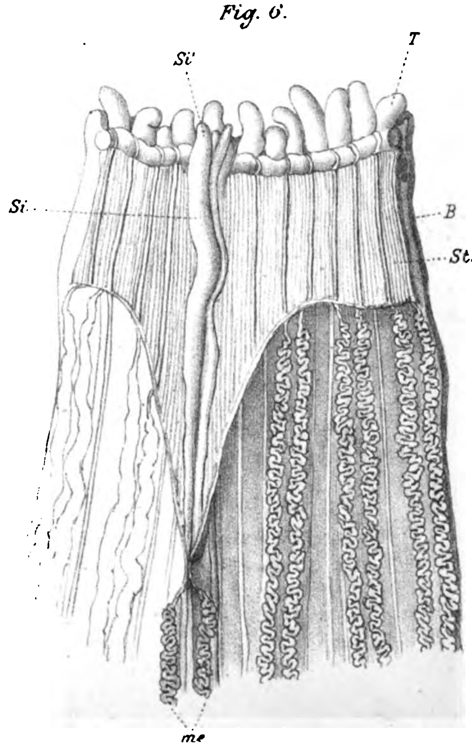


Fig. 6.



...th, Lith^r Edin^r

Fig. 7.

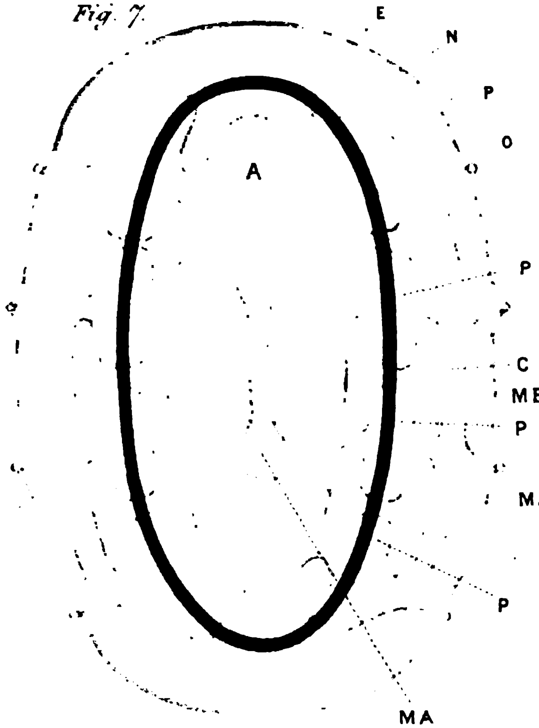


Fig. 8.

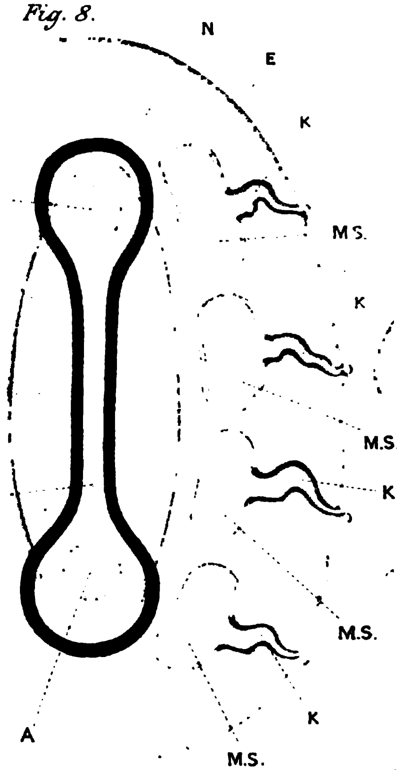


Fig. 15.

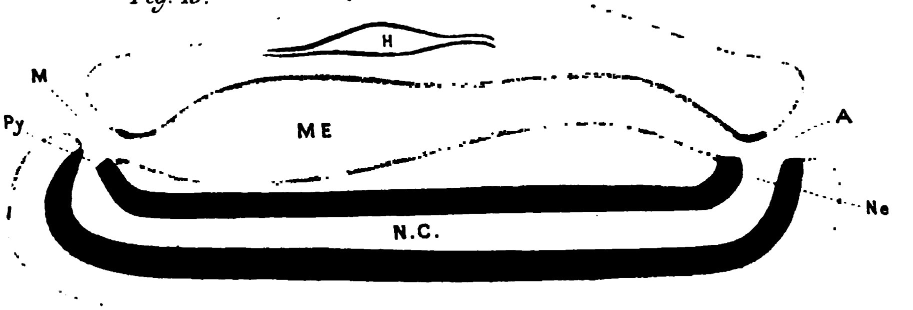
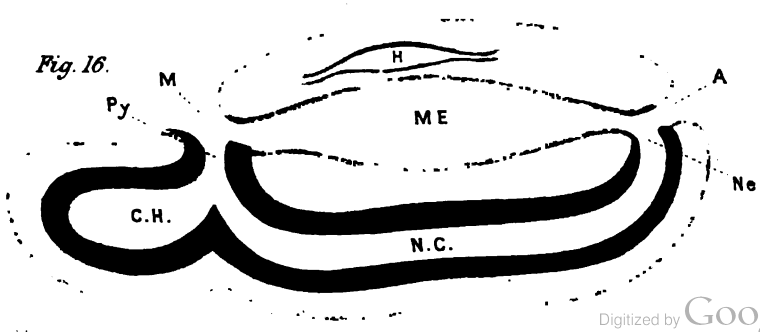


Fig. 16.



10.

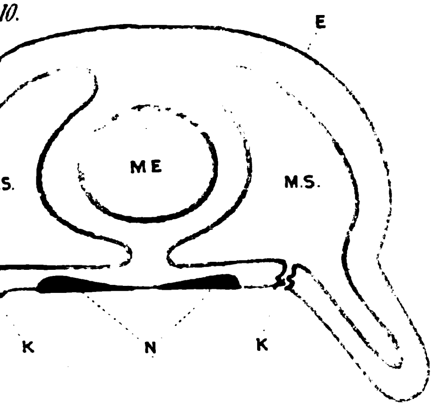


Fig. 11.

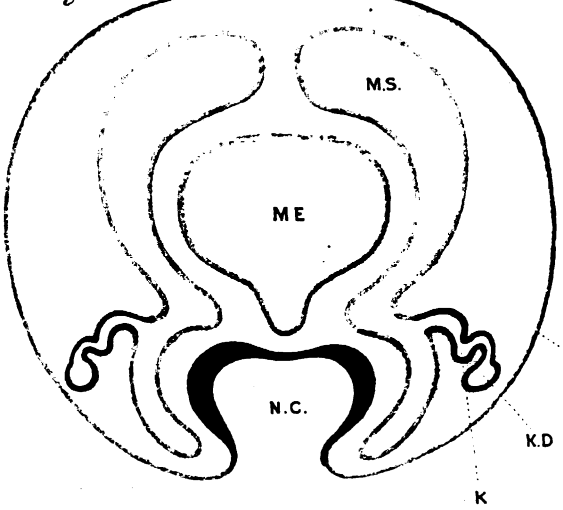


Fig. 9.

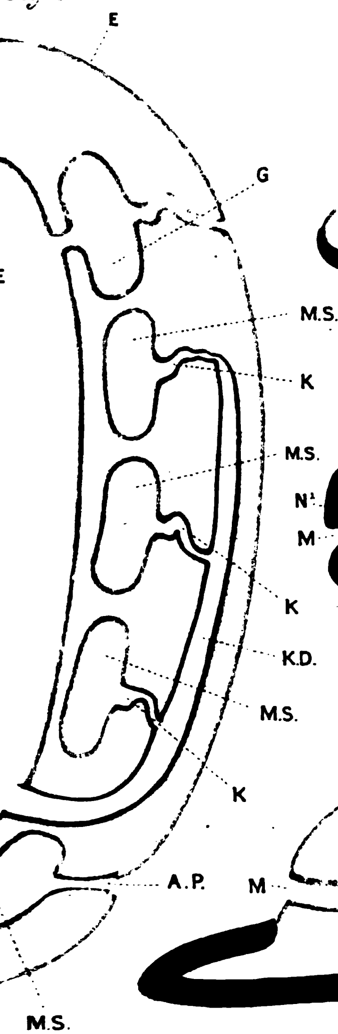


Fig. 12.

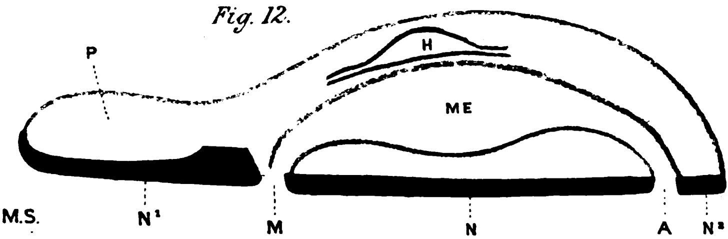


Fig. 13.

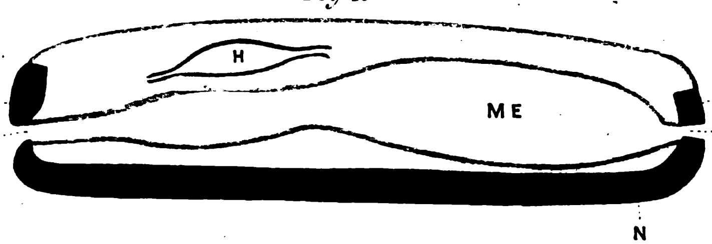
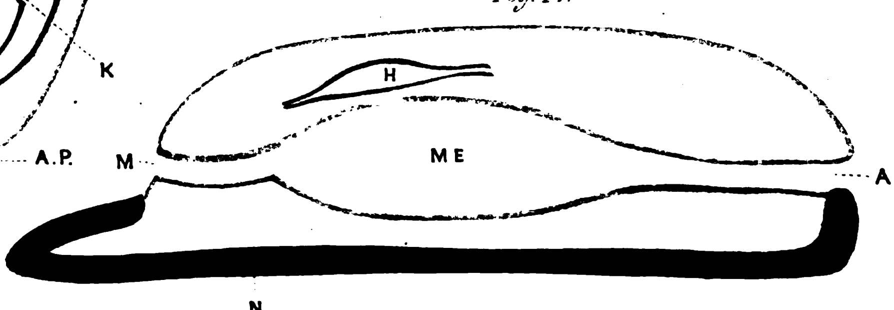


Fig. 14.



F. Huth, Lith^r Ed^n

[redacted] Author's compliments

4

REPRINTED FROM

THE QUARTERLY JOURNAL OF MICROSCOPICAL SCIENCE.

A Criticism of the Cell-Theory; being an Answer to Mr. Sedgwick's Article on the Inadequacy of the Cellular Theory of Development.

By

Gilbert C. Bourne, M.A., F.L.S.,
Fellow of New College, Oxford.

"Jedes Lebendige ist kein Einzelnes, sondern ein Mehrheit; selbst insofern es uns als Individuum erscheint, bleibt es doch eine Versammlung von lebendigen, selbständigen Wesen, die der Idee, der Anlage nach gleich sind, in der Erscheinung aber gleich oder ähnlich, ungleich oder unähnlich werden können. Diese Wesen sind theils ursprünglich schon verbunden, theils finden und vereinigen sie sich. Sie entzweien sich und suchen sich wieder, und bewirken so eine unendliche Production auf alle Weise und nach allen Seiten."—Goethe (1807).

Mr. Adam Sedgwick has of late thrown himself with considerable zeal into the part of a zoological iconoclast, and has displayed an evident relish in battering the idols which, he would fain make us believe, are turning away the minds of men from the true faith, of which there are but few orthodox exponents. Nor may we blame him for his fervour, for an old faith always emerges purer, if not firmer, from the ordeal of sharp antagonism. The idols in question are the developmental law of von Baer and the cell-theory.

Seeing how important a thing it is that a science should be guided by principles capable of being expressed in precise language, it has been a matter of surprise to me that some competent person has not taken up the challenges which Mr. Sedgwick has thrown down. For, if his views are to prevail, two of the fundamental principles of zoology, principles which have hitherto directed and steadied the course of zoological speculation, are taken away from us; and unless some better and more distinct principles are put in their place, the course of speculation may be expected to be very erratic indeed. It is not without serious misgivings as to my own competence that I, in default of a better champion, take up one of these challenges, and I propose to criticise Mr. Sedgwick's recent article on the inadequacy of the cellular theory of development, leaving for a future occasion the consideration of his earlier article on von Baer's law.

It is to be regretted that Mr. Sedgwick should, in putting forward a view affecting one of the fundamental propositions of biology, have chosen to adopt a controversial method, which cannot but have the effect of weakening his case. And it is still more a pity that he should be so unsparing in abuse of his imaginary opponents, whilst he himself commits the very fault for which he so much blames them. For he lays, in the front of his indictment, a charge of vagueness and unsubstantiality against the supporters of the cellular theory. "We are dealing," he says, "with a kind of phantom which takes different forms in different men's eyes. There is a want of precision about the cell-phantom, as there is also about the layer-phantom, which makes it very difficult to lay either of them. Neither of these theories can be stated in a manner satisfactory to every one. The result is that it is not easy to bring either of them to book."

I shall show, later on, that this charge of vagueness is not altogether justified; what I am at present concerned with is to show that Mr. Sedgwick is as much open to the charge of vagueness as the rest of the zoological world which he castigates.

Read his article through as carefully as one may, one cannot find any definite or precise statement of his own standpoint, saving that he quotes passages from one of his earlier works. The critic, therefore, must be content to infer from the tenor of the whole article, and from particular passages in it, as well as from his previous writings, what Mr. Sedgwick does or does not believe with regard to the cell-theory, and if he is misinterpreted, it is his own fault.

It is probably a fair summary of his position to say that, for the present, he limits his objections to the application of the cell-theory to the process of growth during embryonic development; but that he scarcely conceals his preference for the view that there are no such things as discrete cells in the so-called multicellular organism. And as it is necessary, at the outset, to have a perfectly clear idea of his meaning, I will quote passages from the work to which he refers in his opening paragraph, assuming that what he stated then he is prepared to adhere to now, and that his last article is intended to emphasise the views which he formerly propounded, and to bring fresh evidence in support of them.

On p. 204 of the second part of his account of the development of the Cape species of Peripatus, he says:—"It is becoming more and more clear every day that the cells composing animal tissues are not isolated units, but that they are connected with one another. I need only refer to the connection known to exist between connective tissue cells, cartilage cells, epithelial cells, &c. And not only may the cells of one tissue be continuous with one another, but they may also be continuous with the cells of other tissues. . . . It is true that the cells of blood and lymph and the ripe generative cells are completely isolated. But the former, in their first stages of growth, form part of the syncytium, as in all probability do the latter also. This continuity, which for à priori reasons we should expect, has hitherto been regarded as a fact of little morphological importance and relegated to the category of secondary features. The ovum, it is said, segments into completely isolated cells, and the connection between them is a secondary feature acquired late in development. It has always been considered that the first stage in the evolution of the Metazoa was a colonial Protozoon, i. e. a mass of perfectly isolated unicellular organisms, derived by complete division from a single cell. Now while I do not wish to exalt the facts of the cleavage and early development of Peripatus to a position of undue importance, or to maintain that of themselves they are sufficient to destroy this conception of the origin and structure of a Metazoon, I think I am justified in pointing out that, if they are found to be of general application, our ideas on these subjects will have to undergo considerable modification. The ancestral metazoon will no longer be looked upon as a colonial protozoon, but rather as having the nature of a multinucleated infusorian, with a mouth leading into a central vacuolated tract of protoplasm. The continuity between the various cells of the adult—the connections between the nerves and muscles and sensory epithelium, receive an adequate morphological explanation, being due to a primitive continuity which has never been broken. In short, if these facts are generally applicable, development can no longer be looked upon as being essentially the formation of a number of units from a single primitive unit, and the co-ordination and modification of these units into a harmonious whole. But it must rather be regarded as a multiplication of nuclei and a specialisation of tracts and vacuoles in a continuous mass of vacuolated protoplasm."

This is a temperate and lucid statement of a suggestion which is still worthy of serious consideration, the more so since it had been shown, but a short time previous, that protoplasmic continuity between the tissue-cells of plants is of very general occurrence, if not the rule. And, as a historical fact, the continuity of protoplasm was a phenomenon familiar to animal histologists long before it was proved for vegetable tissues; indeed there were authors who, before Mr. Walter Gardiner's researches were published, were disposed to regard protoplasmic continuity as a characteristic of animal organisation, discontinuity as a characteristic of vegetable organisation.

I have quoted at length because Mr. Sedgwick from being temperate has become intemperate, and from being lucid he has become obscure; so that, were I to deal only with his latest utterances, I should be quite at a loss to know what his maturer views might be.

What follows, then, may be taken to be a not unfair statement of his position. That from the connection known to exist between some cells composing adult tissues, there is an antecedent probability that similar connections exist between all cells composing all tissues; and this probability is heightened by observations made on the development of Peripatus, by the fact that the so-called mesenchyme cells in Avian and Selachian embryos are continuous, and not isolated, as was once supposed, and by a study of the developing nerves of Elasmobranchs. And that it follows from this that the morphological concept of a cell, so far from being of primary, is altogether of secondary importance, and that progress in the knowledge of structure is impossible so long as men persistently regard cells as the fundamental structural units on which the phenomena manifested by organised beings depend. The true method of enquiry must be a study of the growth, extension, vacuolation and specialisation of the living substance—protoplasm.

It is in this sense that I propose to deal with Mr. Sedgwick's views, and he will pardon me if I have misinterpreted them. At any rate, I have done my best to understand them.

I would wish to show, in the first place, that there is very slender ground for the accusations which Mr. Sedgwick levels, in an unsparing manner, against his zoological contemporaries. He goes so far as to say that their eyes are blinded by theory to the most patent facts, and that "they are constrained by this theory,"—the cell theory,—"with which their minds are saturated, not only to see things which do not exist, but actually to figure them." This is abuse and not argument; if Mr. Sedgwick were to remember the qualifying sentence in his writings of 1886, "if they are of general application," he would recognise that there is little occasion for accusing zoologists of perversely ignoring the views which he then set forth.

For, in fact, the phenomena to which he draws our attention have received their due meed of recognition from the time that the cellular structure of tissues was first studied. More recent researches have enlarged our knowledge of protoplasmic continuity, but it is still a phenomenon far from being of such universal application as to constrain us to abandon that very useful morphological concept—a cell.

For some years past the study of cells, of their ultimate structure, of their chemical and physical properties, of phenomena which accompany their growth and division, has been carried on with a minuteness which a short time ago was undreamt of. And attention has been directed, not only to the cells composing adult tissues, but in the most marked degree to the successive formation of cells from the primitive unit, the oosperm, and to the fate which each subsequently undergoes in the course of development. In place of the off-hand statements of older embryologists, that the ovum divides into two, four, eight, sixteen segments, and so forth, we have the most accurate and minute accounts of the successive formation of cells, of the place which each occupies in the developing embryo, of its parentage and of its progeny, and of the share taken by the last named in the building up of the adult tissues. In short, we have a number of cell-lineages, which show that in a number of animals, some of which are widely separate from one another, the formation of cells from the ovum follows courses which are either identical or so closely similar that the differences excite our wonder far less than the similarities. So minute are these investigations that every karyokinetic figure has been followed in every cell, up to a stage where their number becomes bewildering.

I refer, of course, to the remarkable series of observations which were begun by Selenka, Arnold Lang, Hallez, Blochmann, and others, and have been carried to the highest perfection by von Wistinghausen, E. B. Wilson, Heymons, and Lillie.

It would be impossible, in such an essay as this, to deal adequately with the results obtained by these authors; and it is unnecessary, since their works are within reach of everyone. It is enough to say here that a perusal of them does not tend to diminish the importance which we have been accustomed to attribute to the cell in developmental processes.

Nothing can be more clear than the fact that, in Nereis or in Unio, there result from the division of the ovum separate protoplasmic corpuscles, as distinct from one another as one room in a house is distinct from another, each of which is not only separate, but contains within itself definite, and probably limited, qualities (at least at stages beyond eight or sixteen cells). One might almost say that, after the earliest stages, each blastomere has a definite task allotted to it, which it faithfully and punctually performs, according to a prescribed course. To each, it might be said in figurative language, is given material, which it must place, not anywhere, but in one particular part of the edifice.

In considering these very remarkable researches, it is not sufficient, for the present purpose, to say that no connection between the blastomeres was observed. Such connections may have existed and have been overlooked; as the connections, which undoubtedly exist, between plant cells were for a long time overlooked. But, a priori, such connections are improbable. For, as has been said, the qualities of each blastomere are limited. Each is specialised before any form changes become visible; each plays one part, and one part only in tissue formation. If their protoplasm were continuous, being made so by uniting strands, then, as Mr. Sedgwick has expressed it, the molecular constitution of any part would in time spread through the whole mass. But the molecular constitution of the blastomeres must be different, for their manifestations are different, and we may possibly see, in this case, some explanation, obscure though it may be, of the isolation of the form elements from one another.

Further than this, there is objective proof that the cells constituting the early embryos of these forms are separate. They exhibit remarkable shiftings of position, which render the existence of connecting strands of protoplasm highly improbable, and the migrations of some cells—e. g. those in Nereis named $c^{1.5.}$ and $d^{1.5.}$ by Wilson—are of such an extent that, if there were protoplasmic continuity, they would be impossible.

It is no exaggeration to say that this is evidence which effectually disposes of the idea that a syncytial theory of animal organisation is of general application.

It does more than this, it shows that there are not a few instances in which cells possess a morphological and physiological significance greater than was at one time supposed.

There are numerous other cases in which, at an early stage of development, cells wander far from the position in which they originated, and become placed so far from the parent cells from which they sprung, that any idea of protoplasmic continuity is impossible. As examples I may mention: the outer layer cells of Cornacuspongiæ and Silicispongiæ, which, as Maas has shown, go through remarkable migrations; the mesoblast of Callianira bialata, Beroe and Cydippe, as described by Metschnikoff, whose statements are confirmed by observations made (but unfortunately not published) by Mr. Riches on Hormiphora plumosa; the lower endoderm cells of Discocœlis, Eurylepta, and Leptoplana, as described by Lang, Hallez, and Selenka.

In short, the evidence is overwhelming, and it must be taken to be very clearly established that there are numerous cases in which there is not "a primitive continuity which has never been broken."

It is apparent, then, that morphologists have been amply justified in refusing to recognise Mr. Sedgwick's views as to the syncytial nature of animals, and there is no justification for the strong language which he uses towards them on account of their refusal.

It is, on the other hand, quite possible that the frequency of the occurrence of protoplasmic continuity between developing tissue-cells may have been overlooked or ignored by a few authors, and that those who have done so have been led into the error of attributing too great and too fundamental importance to the cell as an independent vital unit (Lebenseinheit).

But, in point of fact, I am unable to find, in the writings of any reputable biologist, any statement to the effect that an organism is composed of independent and isolated units. One may, it is true, find passages here and there which, when removed from the context, might be made to bear such an interpretation. I have questioned my pupils with regard to such passages, and I find that they do in fact put such an interpretation upon them. For instance, in Waller's 'Introduction to Human Physiology' the following passage occurs on page 2: "The organism is a community; its individuals are cells; groups of its individuals are organs." Here we have an example of the danger of the too free use of illustrative language. In every illustration there lurks a fallacy. The fallacy may not have been present to the mind of the author; but if the illustration alone is used, without a lucid explanation of its meaning, the fallacy may be the one thing which impresses itself on the minds of his readers. In this case there is a fallacy in the analogy, so often made use of for purposes of popular exposition, between an organism and a community. If the analogy is used without the necessary reservations it leads to confusion, for the reader is only too prone to transfer to the organic unit the idea of the individual isolated man, who is the social unit. The organic unit may in some cases be individual and isolated, but in the great majority of instances it has lost, wholly or partially, its individuality, and is not isolated. It becomes a subordinate part of a higher individality, which in its turn may be subordinate to an individuality of a still higher order. This has been explained in the most lucid and masterly manner by Häckel, in his 'Allgemeine Anatomie der Organismen,' published in 1866; and nobody who has carefully studied that work can fail to have a clear understanding of the subject. Yet it is to Häckel that the doctrine of a cell-republic is often attributed! Clearly by those persons only who have not read his works. For he insists, over and over again, upon a distinction (which since the researches of Mr. Walter Gardiner no longer holds good) between the organisation of plants and that of animals, namely, that the special characteristic of plants lies in the preponderance of the perfected and differentiated individuals of the first order—the cells or plastids. "Der wesentliche tectologische Character der Pflanzen liegt in der vorwiegenden Ausbildung und Differenzirung der Individuen erster Ordnung, der Plastiden" (op. cit., p. 222). Of animals he says, on the contrary, "Der wesentliche tectologische character der Thiere liegt sowohl in der verwickelteren Zusammensetzung der Thierleibes aus weit differenzirten Individuen verschiedener Ordnung, als auch besonders in der verschiedenartigsten Ausbildung der Individuen zweiter Ordnung, der Organe, welche viel mannichfaltiger, als bei den Pflanzen und Protisten, differenzirt und polymorph sind. Die Plastiden, die Individuen erster Ordnung, sind bei Thieren allermeist Zellen, und zwar meistens Nacktzellen (ohne Membran) weniger Hautzellen (mit Membran). Sehr häufig, und allgemein in den entwickelten Personen, vereinigen sich bei den Thieren mehrere Nacktzellen zur Bildung von Zellstöcken (Nervefäsern, Muskelfäsern), was bei den Pflanzen nur bei der Bildung der Milchsaftgefässe und der Spiralgefässe geschiecht. *Daher verliert bei den Thieren stets wenigstens ein Theil Zellen ihre individuelle Selbständigkeit, während sie dieselbe in den Pflanzen meist behalten.*"

The last sentence, which I have put in italics, shows most clearly that, as long ago as 1866, Häckel did not regard the animal organism as a community, whose individuals are cells; and it is the fact that he applied the term "cell-republic" to plants, intending thereby to emphasise the difference which he believed to exist between vegetable and animal organisation.

So that, as a matter of history, whilst plants used to be considered to be colonies of independent life units, animals were not. A certain exchange of opinion seems to have taken place more recently. Some few zoologists and animal physiologists, borrowing from Häckel the term cell-republic, have thoughtlessly applied it, with all its implications, to animal organisation, whilst botanists, influenced by Mr. Walter Gardiner's researches, have insisted more and more upon the individuality of the plant as a whole, and the subordination of its component parts, the cells. None the less, the facts of cell fusion and cell communication have never been wholly overlooked by zoologists, and recent years have brought to light facts, such as the continuity of cartilage cells, which were unsuspected when Häckel wrote.

I am therefore far from being satisfied that the independent-life-unit theory has had such a dominant influence as Mr. Sedgwick would have us believe; and I am quite certain that the picture which he draws of the teaching given to every student of biology is a travesty of the truth.

Biology includes botany as well as zoology, and if we were to allow (which I do not) that zoologists generally have become as narrow in their conceptions of the processes of development as Mr. Sedgwick says, it is quite certain that botanists have not. And as all students of biology are—or if they are not, they ought to be—put through a course of elementary botany as well as of zoology (in many schools the subjects are combined), grave blame must be imputed to those teachers who have, in the later stages of their education, warped the liberal conceptions which they must have formed on the subject of organic growth and development. For I take it that, after a study of Mucor, Vaucheria, and the Myxomycetes, there is no student so dull but he will have imbibed ideas respecting cell growth which impel him to ask the question which as Mr. Sedgwick says it is so difficult to find an answer to—"What, after all, is a cell?" If, when he asks this question, he is told that the cell is an isolated corpuscle of protoplasm, the unit of vitality, and that there is "a most fundamental distinction" between unicellular and multicellular organisms, and so forth, the student may go on his way rejoicing, for that he has at last been given a clear and tangible statement; but none the less he will have been started on a very wrong path. I have not a widespread experience of zoological teaching, but I know, at least, that Professor Lankester's pupils are not started on that path. The truth is, and, if I am not much mistaken, zoologists and botanists alike have long been possessed of it, that there is no fundamental but only a formal distinction between unicellular and multicellular organisms; that the cell is a form concept founded on a very wide basis of experience, whereby we can conveniently interpret to our minds one of the most universal of organic phenomena, viz. the splitting up of protoplasmic masses during growth into a number of more or less distinct corpuscles.

It will not be out of place if I quote here a passage from von Sach's 'Vorlesungen über Pflanzenphysiologie' (English edition, translated by H. Marshall Ward, 1887, p. 73). "To many the cell is always an independent living being, which sometimes exists for itself alone, and sometimes becomes 'joined with others'—millions of its like, in order to form a cell colony, or as Häckel has named it for the plant particularly, a cell republic. To others again, to whom the author of this book also belongs, cell-formation is a phenomenon very general, it is true, in organic life, but still only of secondary significance; at all events it is merely one of the numerous expressions of the formative forces which reside in all matter, in the highest degree, however, in organic substance."

That this is a great limitation of the cell theory, both as propounded by its authors and as held by many zoologists, is not to be denied; and Mr. Sedgwick might well be content if some such statement were made the established doctrine as regards cells. It appears to me that some such limited statement is necessary if we are to have any proposition universally applicable to organic structure; but with this reservation, that I cannot regard as of secondary significance that which all experience shows to be the expression par excellence of organic growth.

In admitting this much, a large part of Mr. Sedgwick's demand is conceded, for it is not to be denied that the cell theory has been very differently and much more dogmatically stated by quite recent authors.

We have, for instance, Dr. Oscar Hertwig's recent work, 'Die Zelle und die Gewebe.' He begins dogmatically enough by saying, "Thiere und Pflanzen, so verschiedenartig in ihren äusseren Erscheinung, stimmen in den Grundlagen ihres anatomischen Aufbaues überein; denn beide sind aus gleichartigen, meist nur mikroskopisch wahrnehmbaren Elementareinheiten zusammengesetzt. . . . Denn die Zellen, in welche der Anatom die pflanzlichen und thierischen Organismen zerlegt, sind die Träger der Lebensfunctionen, sie sind, wie Virchow sich ausgedrückt hat die 'Lebenseinheiten.' Von diesem Gesichtspunkt aus betrachtet, erscheint der Gesammtlebensprocess eines zusammengesetzten Organismus nichts Anderes zu sein als das höchst verwickelte Resultat der einzelnen Lebensprocesse seiner zahlreichen, verschieden functionirenden Zellen." The whole book is written "von diesem Gesichtspunkt aus," and, admirable as it is, there is reason to think that its value is somewhat impaired by the excessive value attributed to the cell as an independent vital unit.

In passing, I may remark that this passage of O. Hertwig's gives a very precise and definite statement of the cell theory, as it is held now, by a very great authority; and a reference to older works would have shown Mr. Sedgwick that, so stated, it is practically the same as what its authors stated.[1]

For the original words of Schwann are these: "The elementary parts of all tissues are formed of cells in an analogous though very diversified manner, so that it may be asserted that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells. . . . . . In inferior plants any given cell may be separated from the plant and can grow alone. So that here are whole plants consisting of cells which can be positively proved to have independent vitality. Now, as all cells grow according to the same laws, and consequently the cause of growth cannot in one case lie in the cell and in another in the whole organism, and since it may be further proved that some cells, which do not differ from the rest in their mode of growth, are developed independently, we must ascribe to all cells an independent vitality; that is such combinations of molecules as occur in any single cell are capable of setting free the power by which it is enabled to take up fresh molecules. The cause of nutrition and growth

[1] "I am not concerned with what its authors held."—Mr. Sedgwick, op. cit., p. 88.

resides, not in the organism as a whole, but in the separate elementary parts, the cells."

The definitions of Hertwig are a re-statement in other words of the salient features of the theory of Schwann, and it is an error to speak of an unsubstantial cell phantom. Nor is there any unsubstantiality about the cellular theory of development, which, I may remind my readers, originated with Remak. The cellular theory of development, taking as its starting point the conclusions of Schleiden and Schwann that all organisms are cells or composed of an aggregate of cells, states that every cell is formed by the division of a pre-existing cell, not as Schwann had supposed, by differentiation within a structureless cytoblastema.[1] Hence Virchow's well-known aphorism, "omnis cellula e cellulâ," which, besides denying abiogenesis, expresses the cellular theory of development as succintly as possible.

It would have been a great advantage to his own argument, and also to his critic, if Mr. Sedgwick had given the clear and authoritative expositions of the cellular theory which lay ready to hand, instead of confusing the issue by a whimsical account of his experience of morphological teaching.

Let us now examine the cell-theory, as stated by Hertwig, in the light of our present knowledge of animal and vegetable structure.

It would not be a difficult task to demonstrate the general truth of Virchow's aphorism. Wherever there is a cell, it may be shown to be the product, and generally the immediate product, of a pre-existing cell. But it would seem that some biologists have added an unwarrantable corollary to Virchow's generalisation, and would say, "Nil nisi cellula e cellulâ." Now from a certain aspect this might be considered true; everything depends on the question as to what is a cell?

Hertwig has pointed out, with much truth, that our present conception of a cell is inseparably connected with our conception of protoplasm. We are still very far from under-

[1] Mr. Sedgwick appears to have leanings towards a cytoblastema, as I shall show further on.

standing the structure of protoplasm, and it might be said that, if we know nothing of the component, it is useless to make assertions about the compost; but it will at least be useful to criticise the attempts which have been made.

Hertwig gives this definition, which is the same as that originally given by Max Schulze. A cell is a corpuscle of protoplasm in which is contained a specially organised constituent, the nucleus. (Die Zelle ist ein klümpchen von Protoplasma, das in seinen Innern einen besonders geformten Bestandtheil, den Kern (Nucleus) einschliesst.) This at first sight seems satisfactory enough, but the more one examines it, the less satisfactory does it appear, in view of the different kinds of organisms which are usually described as single cells.

If a corpuscle containing a nucleus is a cell, is a corpuscle containing two or more nuclei also a cell? And still more, is a large mass of protoplasm containing many nuclei to be regarded as a cell? Such a mass, I mean, as Botrydium, Caulerpa, or Codium, or even Pelomyxa. By many authors these organisms are regarded as single multinucleate cells, but I am far from being convinced that this is a right view of the case.[1]

If there is one thing more than another which has come into prominence as the result of recent research, both botanical and zoological, it is the fundamental importance of the nucleus to cell life. So many minute organisms, which at one

[1] With regard to the argument which follows, I would remind my readers that Häckel, thirty years ago, clearly expressed the view which I am now urging (see his "Allgemeine Anatomie den Organismen," forming the first part of the 'Generelle Morphologie,' p. 296). "Es muss hierbei ausdrücklich errinert werden, dass wir unter eine Zelle nur einen Plasma-Klumpen mit einem Kerne verstehen können. Der häufig gebrauchte Ausdruck einer 'mehrkernigen Zelle' ist eine Contradictio in adjecto, da ja eben nur die Einheit des Kerns die individuelle Einheit der Zelle als eines Elementar-Organismus bedingt. Jeder Plasmaklumpen, der mehr als einen Kern umschliesst, möge er nun von einer Membran umhüllt sein oder nicht, ist eine Vielheit von Zellen, und wenn diese Vielheit eine bestimmte einheitliche Form besitzt, so haben wir sie als Zellenstock zu dem Range eines Organes erster Ordnung zu erheben." This view, however, has been controverted by many authorities, as will appear further on.

time were believed to be non-nucleate, have since been shown to contain nuclei, or at any rate nuclear matter, that we are tolerably well justified in saying that the nucleus, or its equivalent, is an essential constituent of the cell. At all events we know that division of the nuclear substance, whether mitotic or amitotic, is all-important as a prelude to and accompaniment of cell division. The experiments of Gruber and Verworn show that if Amœbæ are artificially divided, the parts cut off will regenerate and lead an independent existence if they contain nuclear matter, but if they do not, they soon perish. Fragmentation of the nucleus—by which is produced a so-called multinucleate condition, often of considerable duration—is a prelude to spore formation, i. e. to the division of the cell into many parts. Mitotic division is highly characteristic of division of the cell into two parts. It is very difficult to draw distinctions, but it is worth consideration whether the temporary multinucleate condition ending in multiple fission, which is common in protozoa, has not a different value to the permanently multinucleate condition of some plants and animals, which are generally called unicellular. In the one case (e. g. Podophrya, Thalassicolla, Actinosphærium) division or fragmentation of the nucleus leads, sooner or later, to the separation of cells, each containing a fragment of the original nucleus. In the Cœloblastæ (Siphoneæ, e. g. Caulerpa) the repeated division of the nucleus is not followed by any cell division, but the organism is throughout life a mass of continuous undivided protoplasm. The plant, as von Sachs says, is of considerable size, develops roots, even leaf-forming shoots, and in its protoplasm hundreds and thousands of cell nuclei are contained, which with advancing growth are multiplied by division, and obtain a definite arrangement within the protoplasm. And, as in the case in cellular plants, the nuclei are specially aggregated at the growing points. The whole behaviour is just that of a multicellular plant, but there are no partition walls.

It is stretching the point very far to call this a single cell. And, in fact, it is an inconsistency to do so, for where, by an essentially similar process, a continuous sheet of protoplasm containing many nuclei is formed as a tissue-constituent of a multicellular animal or plant, we do not call the whole multinuclear tract a single cell—we call it a syncytium, or take some roundabout way of describing it. Such a case is the formation of the endosperm in the embryo-sac of Phanerogams. By repeated mitotic division of the nucleus and growth of the surrounding cytoplasm, a tract of continuous protoplasm is formed, containing many nuclei. At a later stage partitions are formed and the mass is divided up into cells, but for a period the endosperm has a structure which recalls that of the Cœloblastæ. Can we say that the condition in the endosperm is to be regarded as multicellular because it is not permanent, and that the condition in the Cœloblastæ is to be regarded as unicellular because it is permanent? If this is allowed the consequences are far-reaching, for it follows that the multinuclear phase in Actinosphærium and other Protozoa is also multicellular, because not permanent.

Take, again, the case of the Mycetozoa. The plasmodium of Badhamia or Fuligo is not unicellular, for it is formed by the union of many cells: it is not called multicellular, because there are no cell divisions: yet we draw, rightly enough, a distinction between the plasmodium, where cell bodies fuse but the nuclei do not unite, and the single cell resulting from conjugation, where the nuclei do unite.

A survey of the facts must lead to the conclusion that there is an intermediate phase between the unicellular and the multicellular condition, which is the multinucleate but non-cellular condition,[1] and that there is no fundamental distinction

[1] The term non-cellular does not exactly represent the condition which it is intended to describe. Yet, if one adheres to existing nomenclature, it is difficult to find a substitute. The term "cell," though founded on an erroneous conception, is so firmly established in biological language that it would probably be impossible to eject it. Yet if one were to make general use of the Greek equivalent κύτις (literally a little box), which has already come into such favour as to have respectable claims on our attention, one might adopt much more exact expressions. Thus the uninucleate Protozoa might be said to exhibit a monocytial condition, multicellular organisms a

between Protozoa as unicellular, and Metazoa as multicellular organisms. I should hardly have thought it worth while to insist upon this had not Mr. Sedgwick written "that an organism may consist of one cell or of several cells in association with one another. We draw the most fundamental distinction between the two kinds of organism, and we divide the animal kingdom into two great groups to receive them. As a proof of the importance which we attach to this feature of organisation we assert that a man is nearer, morphologically, to a tapeworm than a tapeworm is to a paramœcium."

Botanists, who have the great advantage of studying the physiology concurrently with the morphology of their subject, make no fundamental division into Protophyta and Metaphyta. For them, unicellular plants, hypopolycytial plants, Fungi and Algæ are alike Thallophyta, and a passage from Goebel may serve to illustrate the point of view which leads them to classify together organisms which, from the point of view of "independent life units," would appear widely separate. "From this initial stage"—a single small cell—"the process of development may advance, yet still within the limits of a single cell, and whilst the cell increases in size, often reaching dimensions without parallel in the vegetable kingdom, either the differentiation of the cell-contents or that of the external form, as shown by the branching, may make most rapid progress. In other cases the growth of the cells is accompanied by cell-division, the thallus becoming multicellular, and the single cell producing, according to the nature of the plant, a cell row, or a cellular filament, a cell surface or simple tissue layer, or lastly a cell mass increasing in every direction."

polycytial condition, and the so-called non-cellular condition of Cœloblastæ and Opalina might appropriately be called hypopolycytial, the preposition ὑπὸ being used in a modifying sense, as expressing the intermediate stage between one and many. The term syncytial, which is now used in a loose sense, is strictly applicable to the early condition of the plasmodia of the Myxomycetes, which are formed by the fusion of many units in a monocytial condition, and are therefore different from organisms which exhibit a hypopolycytial condition. In later stages the nuclei of the plasmodia multiply by division; thus the hypopolycytial is added to the syncytial condition.

Although in this passage, which is descriptive of Thallophytes, Goebel attaches too much importance, as I think, to the continuity of a vesicle as determining the unicellularity of a plant, he shows clearly enough that he regards the growth and mode of extension of the protoplasm, not its division into cells, as the feature of fundamental importance.

There is the further property in plants that continuity between the cells of highly organised multicellular plants has been shown to be of very general, if not universal, occurrence. And if complete separation were to be insisted upon as a characteristic of a cell, any given Angiosperm, or other highly organised plant, could no longer be considered as an aggregate of life units, but rather as a conjunct mass of protoplasm, imperfectly broken up into corpuscles, in each of which there is a nucleus. It is but a step from the much-branched, multinucleate Cœloblastæ, which have no partitions, to the formation of incomplete partitions, breaking up the protoplasm into small masses, which remain, however, linked with one another, and so preserve an original continuity similar to that of the Cœloblastæ, which has only apparently but never actually been broken.

So much has this idea impressed itself on the minds of some observers, that Hofmeister suggested that the creeping motion of the plasmodia of the Myxomycetes and their later transformation into fructification, is representative of the simplest type of growth, even for more highly organised plants. This opinion has been quoted with approval by von Sachs, who, before even the continuity of the protoplasm of plant cells was established, wrote that "fundamentally every plant, however highly organised, is a protoplasmic body, coherent in itself, which, clothed without by a cell-wall and traversed internally by innumerable partitions, grows; and it appears that the more vigorously this formation of chambers and walls proceeds with the nutrition of the protoplasm, the higher also is the development attained by the total organisation."

Expressed in this way, the phenomenon of cell-formation is represented to us as being nothing more than a particular manifestation of growth, and Mr. Sedgwick may contend that his views are thereby conceded, and that the ancestral metazoon may, on this aspect, be considered as "a multinucleate infusorian with a mouth leading into a central vacuolated mass of protoplasm." There may be truth in the contention, yet none the less we may hold fast to the concept of a cell, as I shall attempt to show further on. And it may be observed in passing that Mr. Walter Gardiner, in describing and emphasising the continuity of protoplasm in plants, expressly stated "that the presence of minute perforations of the cell-wall need not lead to any modification of our general ideas as to the mechanism of the cell," a proposition which most reflective persons will be cordially inclined to agree with. For this much is certain, that the formation of cells is not merely the expression of one out of many formative processes which reside in organic matter, but is the formative process, par excellence, which obtains both in animal and vegetable tissues.

Thus far I have endeavoured to show that the independent-life-unit theory has not held the minds of zoologists in an iron bondage, much less the minds of biologists, for, when reference is made to biologists, botanists must be taken into equal account with zoologists.

It is, however, arguable that, whatever botanists have thought, zoologists have not followed their example, but have publicly maintained a complete adherence to the independent-life-unit theory in its most limited form, whatever reservations they may privately have made in their own minds.

But it may be doubted whether the argument holds good. I have already shown that passages which seem to state most dogmatically that cells are separate individuals, prove on examination to be nothing more than illustrations; and it is to be remembered that ideas founded on botanical evidence must always be reflected on the minds of zoologists, and one may certainly say that conceptions of animal structure have of late years been considerably modified by the light thrown upon organic structure in general by botanical investigation. Some zoologists may possibly have given too little attention to growth without division into cells, because there are not in the animal kingdom any such striking instances of massive growth without cell division as are exhibited by the Cœloblastæ, especially if we leave out of consideration the Mycetozoa, as belonging to the debateable territory between the two kingdoms. Nevertheless, we have instances of growth and mitotic nuclear division, unaccompanied by cell division, which are not apparently a mere prelude to division. Take the single instance of Opalina ranarum. Because this organism is microscopic, and may be described, without offence to our sense of proportion, as a corpuscle, it is invariably called unicellular. Yet in essential features it resembles one of the Cœloblastæ. It contains numerous nuclei, which divide mitotically, and their division is an accompaniment of the growth of the mature organism. The multinucleate mature condition is of considerable duration. In the reproductive process this multinucleate corpuscle divides repeatedly, until a number of small offspring are formed, each containing several, usually four or five, nuclei. The minute product of fission then encysts, and it is remarkable that either during or immediately after encystment the several nuclei break up, and a single new nucleus is formed,—presumably it is constituted out of the chromatin of the several nuclei. The form which emerges from the cyst grows, and growth is accompanied by repeated mitotic division of the nucleus till the mature condition is reached. The whole history reminds one of that of a Mycetozoon, except that the young do not fuse to form a plasmodium, but simply grow up; in this respect Opalina resembles the Cœloblastæ, differing from them, however, in the fact that the whole organism is concerned in reproduction, not a special part. Although it has, as he remarks, a distinct "development," Zeller, who first followed its life history, has no doubt that Opalina is a single cell.

Now the multinucleate condition is far from uncommon in the Protozoa, and it may almost be said to be the rule in the Ciliata, if we regard macronucleus and micronucleus as two separate nuclei. But putting aside this phenomenon, the significance of which we do not yet clearly understand, there are several Ciliata which have as many as one hundred nuclei, e. g. Holophrya oblonga, Lagynus elongatus, and Uroleptus roscovianus.[1] I do not include as multinuclear those forms in which, as in Trachelocerca phœnicopterus or Chœnia teres, the chromatin is scattered throughout the protoplasm in the form of minute granules. Those Protozoa only may be considered multinucleate in which there are several well-defined aggregations of chromatin. And even if the Ciliata above mentioned may not be considered truly multinucleate, but to possess only a fragmented nucleus, there can be no doubt about some Amœbæ, e. g. Amœba quarta and others described by Gruber.[2] In the last-named the multinuclear state is constant; as Gruber says, "es sich nicht etwa um vorubergehende Entwicklungszustände handelt." He watched these Amœbæ for a long period, expecting that the large number of nuclei would at last find its explanation in reproduction by multiple fission, but he was unable to observe any such culmination. Dr. Gruber is a great authority, and he, equally with Zeller and others, is quite positive that the multinuclear Protozoa are truly unicellular. His reasons are, that closely allied species are uninuclear, and that the protoplasmic body is continuous—contained in the case of Ciliata by a single cuticular coat. But even he admits that the only reasonable interpretation of the multinuclear condition is that it is a prelude to reproduction, that is, to cell division.[3] It is, therefore, a condition intermediate between the unicellular and the multicellular condition, or, as I should like to call it, a hypopolycytial condition, and nothing more need be affirmed of it.

Zeller is quite precise as to his reasons for regarding Opalina as unicellular. "Die kleinsten Thierchen aller bekannten Opalinen, so wie sie von Neuem sich zu entwickeln beginnen, besitzen nur einen einfachen Kern und entsprechen

[1] Maupas, "Études des Infusoires ciliés," 'Arch. Zool. exper. et gen.' (2), i, 1883.

[2] 'Zeit. für wiss. Zool.,' xli, p. 186.

[3] Aug. Gruber, "Ueber vielkernige Protozoa," 'Biol. Centralblatt,' iv, p. 710.

unzweifelhaft, wie Engelmann schon für die von ihm untersuchte Art nachgeweisen hat, 'morphologisch vollständig einer einzigen Zelle.' Aber auch mit der weiteren Entwicklung ändert sich daran nichts. Mag die Zellhaut zu einer aus vielen einzeln zerlegbaren Bändern bestehenden muskulöses Hülle werden und mag der Kern in zwei Kerne zerfallen, wie in O. similis und O. caudata, oder durch fortgestzte Theilungen eine schliesslich sehr grosse Menge von Kernen aus sich hervorgehen lassen, wie in O. ranarum, O. obtrigona und O. dimidiata, *die protoplasmische Körpersubstanz selbst zeigt keine weitere Veränderung als die der Massenzunahme und blebt, wie auch Engelmann hervorhebt, 'Zeitlebens eine einzige zusammenhängender Masse, wie von eine einzigen Zelle.'"* I have put the last passage in italics, because it expresses most clearly why Zeller and other authors regard multinucleate forms as unicellular, namely because the protoplasm shows no other change than increase in size, and because it remains, its life long, a single continuous mass. The same argument leads many to regard the Cœloblastæ as unicellular. The continuity of the protoplasm, then, is the test of unicellularity.

If anybody accepts this, he cannot escape from its logical consequences. Not only are multinucleate Protozoa and Cœloblastæ unicellular, but also the whole kingdom of plants, for their protoplasm is continuous: the developing Peripatus is unicellular, for its protoplasm is continuous; the epithelial cells of many animals, as Max Schulze, Pfitzner, Klein, Paulicki, Th. Cohn, and others have shown, are united by fine protoplasmic processes much as are the cells of plants, therefore the epithelia are unicellular, for their protoplasm is continuous. The same may be said for muscle cells (Werner and Klecki), for connective tissue, for bone cells, for the developing mesoblast of Vertebrata (*teste* Sedgwick, Assheton, and others), for the mesoblast (mesenchyme) of trochospheres and Molluscan larvæ (see particularly von Erlanger), and for many other tissues.

Thus the inevitable result of an argument which is meant by those who use it to tighten the bonds of the cell-theory is to loosen them altogether, and to hand us over unbound to Mr. Sedgwick, who would fetter us once more with a new doctrine, viz. there is no cell, all organisation is a specialisation of tracts and vacuoles in a continuous mass of vacuolated protoplasm.

We do not want to be bound, at least I do not, and if we are to be free we must take refuge in some such lax but comprehensive statement as that of von Sachs, viz. that cell formation is a phenomenon very general in organic life; but even if we must regard it as only of secondary significance, it is the characteristic expression of the formative forces which reside in organic substance.

Now this statement affirms the existence of cells, and it is necessary to arrive at some understanding as to what is a cell; what properties are connoted by this term?

It has become abundantly evident in the course of this argument, that whatever other attributes may be affirmed of the cell, the possession of a nucleus is one of the most important. It is impossible to disagree with Pfitzner when he writes, "Wenn wir aber den Kern überall und zwar immer und in allen Stadien als durchaus selbständiges Gebilde finden, so ergiebt sich deraus dass er fur das Bestehen der Zelle als solchen ein Organ von wiel fundamentaler Bedeutung ist als wir bisher geneigt werden anzunehmen." This is also the view of O. Hertwig, and it is no new one, for Max Schulze insisted upon it, and Häckel wrote in 1866, "Ein Plasmaklumpen ohne Kern ist keine Zelle mehr."

But can we follow Pfitzner when he goes further and says, "bei einer so ausserordentlich Konstanz in der ganze Reihe der Thierformen, von den Protozoen bis zu dem Menschen, kann ich nicht umhin auzunehmen dass überhaupt die ganze Existenz eine Zelle als biologische Einheit an das Vorhandsein eines centralen Körpers, von komplicirten inneren Bau, gebunden ist, dass also die Chromatinstrukturen nicht etwas sekundären erworbenes, sondern die Grundbedingung vitaler Existens der Zelle darstellen. Und weiter folge ich hieraus das der als Karyokinese bezeichnete Vorgang nicht ein specielle Kerntheilungsmodus, sondern der Kerntheilungsmodus κατ᾽ ἐξοχήν ist"?

I think not. Particles of chromatin scattered through the protoplasm do not constitute a nucleus any more than a heap of bricks constitutes a house. Under such a view, Ciliata like Trachelocerca phænicopterus and Chænia teres would not be cells, for they have no central nucleus of complex structure, nor have Oscillaria and Bacterium, in which chromatin granules have been discovered. Though the case of Holosticha scutellum, in which scattered nuclei (chromatin particles) unite and fuse to form a single central body or nucleus previous to division, may help to clear our ideas, it is evident that the demand for a central organised constituent is more than the cell conception can bear, especially if the demand carries with it a further demand for the universality of mitotic division in nuclei.

In short, before we could accept Hertwig's definition of a cell, we should have to ask and answer the question, What is a nucleus?

Here I may stop to ask whether it is worth while to discuss the grounds of a definition which, when made, could not be acceptable to the mind of everyone. An argument about definitions would soon land one in the regions of scholasticism, and I have no desire to enter into subtleties which would tax the powers of a Duns Scotus. To give an answer which shall be beyond all cavil to the question, What is a nucleus? would be about as easy as to answer how many angels can dance on the point of a needle.

The truth is that it is the attempt to frame short concise definitions, applicable without exception to whole classes of phenomena, which leads to trouble. The concepts of biology may and should correspond with the phenomena we observe, but they can very seldom be made into universal propositions. There is no place in the science for definitions as exact and universal as those of geometry. The qualities of a nucleus are not to be defined like those of a point or a line. Such propositions as we may make are but resting-places for our minds as we ascend the mazy scale of organisation. To attempt to form definitions, to predicate the precise attributes of whole classes of phenomena, is to run counter to the very genius of the subject. For what do we mean by evolution if not that life is labile, never resting, protean in its variety? And how can we express this but in an incomplete way, contenting ourselves with particulars, and trying to show that the stream, though it flows in many tortuous channels, is one stream nevertheless.

Cells and nuclei are protean in their variety, and since we very rightly insist on objective study as a preliminary to the understanding of them, it is not wonderful that they should give rise to this concept in the mind of one man, and to that concept in the mind of another man, and thus it is not surprising that the theory of cells should be incapable of being stated, as Mr. Sedgwick complains, "in so many words in a manner satisfactory to everyone."

It is fairly obvious that Mr. Sedgwick's quarrel with the cell-theory began with the dissatisfaction which he felt when he discovered that doctrines, which he believed to be of universal application, were in fact contradicted by several instances. But he fell out of Scylla into Charybdis when he supposed that he could reply to a universal affirmative by a universal negative.

There is an old and respectable rule of logic that of two contrary propositions both cannot be true and both may be false, whilst of two subcontrary propositions both may be true but both cannot be false. Had Mr. Sedgwick remembered this, he would not have attempted to overthrow the cell-theory by the statement of a contrary proposition of equally universal import.

The cellular theory of development in the popular form in which it is often presented may be briefly summed up somewhat as follows. The multicellular organism is a colony, consisting of an aggregation of separate elementary parts, viz. cells. The cells are independent life units, and the organism subsists in its parts and in the harmonious interaction of those parts.

The falsity of this summary is evident when we consider the known facts of vegetable organisation; the development of Peripatus; the union, by means of protoplasmic processes, of epithelial, muscular, and connective-tissue cells; the evidence lately adduced as to the continuity of the mesoblast in Elasmobranchs, Aves and Mammalia, and other well-known instances.

The absolute contrary, as expressed by Mr. Sedgwick, is equally false, viz. that the metazoon is a continuous mass of nucleated vascular protoplasm, subsisting in the unity of its mass. For, as I have shown in the earlier part of this essay, there are unequivocal instances of distinct isolated cells occurring in the embryos of many Metazoa (Nereis, Unio, Umbrella, Leptoplana). Moreover I am convinced, by my own studies on the histology of Cœlenterates, that, whilst there is organic connection between many of the tissue-cells composing these organisms, as was demonstrated long ago by the brothers Hertwig, there are many other cells of which such continuity cannot be affirmed.

To deal clearly with the cell-theory, or rather with the independent-life-unit theory which has grown out of it, we must split it up into as many separate propositions as it contains. These are:

The multicellular organism is an aggregate of elementary parts, viz. cells.

The elementary parts are independent life units.

The harmonious interaction of the independent life units constitutes the organism.

Therefore the multicellular organism is a colony (cell-republic according to Häckel).

It is not necessary to follow the theory further into the consequences which are deducible from these propositions, e. g. that development consists in the separation of numerous individual units from a single primary unit, the ovum. It is obvious that the truth of the first proposition in no way depends on the truth of those which follow, and that, in fact, the second proposition is an assumption which is made to explain the first. We may make Mr. Sedgwick a present of the last three, whilst we retain and value the first.

The essence of the whole question is this: are we justified in considering the elementary parts of an organism to be independent life units? Before we can answer this, we must inquire why we do consider them to be independent life units?

The answer to this is probably to be found in the aphorism, which commends itself to everybody, that reproduction is discontinuous growth. From the observation that, in unicellular organisms, division of the unit—the cell-corpuscle—leads to the liberation of a new and independent unit, and that in multicellular organisms it is the liberation of an independent unit—the ovum—which constitutes reproduction, it has become a settled conviction in men's minds, that division of a cell-corpuscle means the liberation of a new unit, that is, the setting free of a new independent being. It is this conviction which has led to the belief that the units composing a multicellular organism are in posse independent beings, though in esse subordinate to the whole of which they form a part. This was the argument of Schwann when he wrote the passage which I have quoted on p. 149, and the argument has been taken as conclusive.

But we know now that the power which Schwann and his followers limited to cells is inherent in protoplasmic masses not divided into cells. For instance, if the cell-membrane of a Cœloblastic alga is ruptured, portions of the exuded protoplasm, provided they contain one or more nuclei, may become, after a time, surrounded by a new cell-membrane, grow, and form a new plant.

The experiments of Gruber show also, that portions of Amœbæ artifically separated may, provided that they contain nuclear substance, recover from the operation, and lead an independent existence.

May I ask, in parenthesis, whether there can be a better illustration of the truth of the contention which I have endeavoured to establish above, that whilst a uninucleate corpuscle of protoplasm is *in esse* as also *in posse* a unit of independent vitality, a multinucleate corpuscle or mass of protoplasm is *in posse* composed of separate cells (units of independent vitality if one chooses to call them so) whilst still *in esse* a single unit of independent vitality?

To continue the subject. We now know also that division into cells is not necessarily, though it sometimes may be, division into units of independent vitality, but is often (may we not say generally?) incomplete separation into form elements which may indeed, under certain conditions, be completely separated, and exhibit an independent vitality (Begonia), but under normal conditions participate in the vitality of the whole plant or animal by means of their connections with their fellows. Hence we must conclude, as it seems to me, that the elementary parts of organisms are not independent life units *in esse*. They may be so *in posse* in many cases, but as differentiation and specialization progress they lose this power also, and cannot, when separated from the whole of which they form a part, exhibit independent activities.

This consideration leads to the apparent paradox, that the higher the organisation the less conjunct and, at the same time, the less independent are its parts; the lower the organisation the more conjunct, but also the more independent are its parts.

This is a puzzle which has, for years past, exercised the minds of biologists. There is, I believe, but one solution of the difficulty, and it is to be found in the physiological import of cells.

But before we can enter into this question we must finally satisfy ourselves, as far as circumstances allow, about the morphological concept of a cell.

That the cell is a thing cognisable, and that it is not an unreal figment, due to imperfect observation or to hopelessly prejudiced interpretation of our observations, as Mr. Sedgwick would make us believe, I will try to show.

A cell is a "body," and therefore an external cause to which we attribute our sensations. I would submit that, without prejudice to the metaphysical standpoint, we must conceive that what is capable of giving rise in us to such very distinct sensations, must have a real existence. I am referring now to the component parts of the tissues of higher animals and plants, and not to unicellular organisms.

If, then, the thing has existence, it must have attributes; we must be able to affirm something of it. What we have to affirm is not the attributes of this cell or of that cell, but of cells in general. We have to give expression to a morphological idea, in the sense in which Goethe used the word morphological. Our concept of a cell must be an "Allgemeines bild," the generalised idea of a cell, derived from our experience of many kinds of cells. I have already shown, at sufficient length, that we must now regard something of the nature of a nucleus as an essential component of all cells, but as the concept of a nucleus as a central organised body is not applicable to all cells, I would widen Max Schulze's definition by saying that "a cell is a corpuscle of protoplasm, which contains a specialised element, nuclein." This is a sufficiently comprehensive statement of our "Allgemeines bild," though I cannot pretend that it is not open to objection.

Cells, as thus defined, are not only of various kinds, but they are variously compounded together. We may, by the process of dichotomous division, classify them, according to their relations to other cells, as discrete and concrescent.

By discrete cells, I mean those whose protoplasm is not in union with that of any other corpuscle.

By concrescent cells, I mean corpuscles whose protoplasm is in union with that of other corpuscles.

Discrete cells may further be divided into:

Independent cells, living wholly apart from one another, or separated by an appreciable interval of space, e. g. uninucleate Protozoa, the mature ovum, leucocytes.

Coherent cells, which are in close apposition to others, but not organically in union with them, e. g. the blastomeres of many developing embryos.

Concrescent cells may also be further divided into:

Continuous cells, whose protoplasm is fused but whose nuclei are separate, e.g. Myxomycetes, Cœloblastæ, Opalina.

Conjunct cells, those which having a protoplasmic body of definite outline are united inter se by fine bonds of protoplasm, e.g. vegetable tissue cells, epithelial cells of many animals; mesenchyme cells, &c.

Experience shows us that independent cells may, in process of growth, give rise to coherent cells, continuous cells, conjunct cells, or to all three together, and that coherent, continuous, or conjunct cells may, and in fact do, give rise to independent cells. As thus stated, can there be a better illustration of von Sachs's principle that cell-formation is an accompaniment of growth?

It will be observed that, in adhering to the present terminology, I am obliged to classify organisms usually (though not always) called unicellular as multicellular. I have tried to escape from this necessity, but the limitations of language compel me to it. I should be grateful for a better and more logical definition.

The view of Mr. Sedgwick—if I do not misrepresent him—is this, that there are no coherent cells; that all which I have classified as continuous and conjunct cells are not cells, but tracts of protoplasm; that the only cell, sensu stricto, is the independent cell, and that morphologically and physiologically it is of no consequence.

I have already shown that there are cells which we must regard as coherent. I cannot, for reasons which I will explain directly, consider the independent cell of no consequence, and the difference between us as to conjunct cells is simply this: Are they to be regarded as one or many? I can, perhaps, best express this difference by an illustration.

Is a house to be regarded as one room or composed of separate rooms? A room is a certain portion of space enclosed by walls, ceiling, and floor; but it is also in connection, by means of the door, with other similar rooms. Is it, then, not a separate room, but part of a larger room? Or if I shut the door is it a room, and if I open the door is it no longer a room? The subject might be argued with much ingenuity, but the final answer is this—that "room" and "cell" are terms which give expressions to certain states of our consciousness, and for practical purposes they are very useful terms indeed. Where distinct states of consciousness are called up, of such a nature as to give rise to ideas of particularity, it is a mere quibble to argue that the apparent parts are actually merged in a whole. A cell is none the less a cell, in the sense of a thing distinct in itself, because it is conjunct with its fellow cell, than my room is the less a room because it has one door opening into an adjoining room and another opening into the passage.

Yet there is something more than a verbal quibble in Mr. Sedgwick's contention. He would have it that in the case of mesenchyme it is incorrect to say that it is a number of stellate cells joined to one another by their processes. For him the correct description is, "a protoplasmic reticulum with nuclei at the nodes." Does he accept the logical consequences of this, and say of the epithelial cells of the Salamander or of unstriped muscle fibres that they are protoplasmic reticula with nuclei at their nodes? And if so, how does he explain the fact that, in the one case and in the other, the elements when absolutely isolated by appropriate methods show a remarkably constant and characteristic form? Were they what he describes, rupture of the internodes of the reticulum would result in amorphous lumps of protoplasm, not in units of characteristic form. It is the constancy of the various forms of cells which convinces morphologists of their individuality as form elements, and all the arguments which Mr. Sedgwick or anybody else may choose to bring forward will not convince the man who goes into a laboratory, makes a few maceration preparations, and studies the results for himself.

Thus a tissue formed of conjunct cells is made up of many and not of one, and as a form concept the cell holds its ground and, pace Mr. Sedgwick, it will continue to hold its ground against all comers.

As a physiological concept it is hardly less useful, though reflection may induce us to abandon the "cell-republic" theory, as, indeed, it has been tacitly abandoned by many. I take it that the scheme of von Sachs very nearly expresses, in general terms, the physiological importance of the cell. An organism is a protoplasmic body, coherent in itself, which grows, and as it grows it is divided by cleavage into innumerable corpuscles, and it appears that the more vigorously this formation of corpuscles proceeds with the nutrition of the organism, the higher also is the development attained by the total organisation. Nor does this statement stand in any contradiction to the original theory of Schwann, from whom I may quote two more passages: "The elementary parts of all tissues are formed of cells, in an analogous though very diversified manner, so that it may be asserted that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells." And again, he says of the relations of cells to one another, "Each cell is within certain limits an individual, an independent whole. The vital phenomena of one are repeated, entirely or in part, in all the rest. These individuals, however, are not ranged side by side as a mere aggregate, but so operate together in a manner unknown to us, as to produce a harmonious whole." It should be remembered that Schwann regarded cells as so many separate vesicles, and when allowance is made for this error, the second part of the last passage must be allowed to have great significance. The subordination of the parts to the harmonious whole, leading to the loss of individuality of the parts, in animal tissues, was insisted on by Häckel in his 'Generelle Morphologie.' The first of the two sentences which I have quoted from Schwann is even more true to-day than when it was written, for we have got rid of the cell-forming matrix, the cytoblastema; and I would wish to insist on this passage as expressing in the clearest possible language the cell-theory as we understand it to-day.

From this standpoint we can see, obscurely it may be, why cell-formation accompanies differentiation with growth of the mass, and why specialisation is not possible in continuous tracts of protoplasm. For, as Mr. Sedgwick himself admits, in a continuous mass of protoplasm, changes of molecular constitution in any one part would in time spread through the whole, so that a differentiation of one part would in time be impressed on all the other parts, and physiological division of labour would be out of the question. The fact that in the Protozoa there is differentiation within the limits of a single corpuscle presents no greater difficulty than the fact that in the epithelio-muscular cells of Cœlenterates, or the similar cells in Nematodes, there is differentiation within the limits of the cell.

Again, metabolism in a large mass is greatly facilitated by its being broken up. As von Sachs says, "It is very intelligible that not only the solidity but also the shutting off of various products of metabolism, the conduction of the sap from place to place, and so forth, must attain greater perfection if the whole substance of a plant is divided up by numerous transverse and longitudinal partitions into cell chambers." The same thing applies, mutatis mutandis, to animals, and it is not difficult to see that the difference between holozoic and holophytic nutrition makes it impossible for the animal to grow to a large mass without division into cells, whilst such growth is possible in the case of plants which, like Codium and Caulerpa, live in water, or like Botrydium in damp earth.

It is known that the spaces between epithelial cells which are traversed by the connecting strands of protoplasm, and were formerly supposed to be occupied by a cement substance, are in reality lymph spaces, and this gives us some insight into the importance of the cell structure in animal organisation. The formation of cells with spaces between admits of nutrient fluid being brought to the very threshold of each constituent corpuscle of the organism. (See on this subject Th. Cohn, R. Heidenhain, Paulicki, Nicolas, Werner, and others.)

Whilst the necessities of cohesion, solidity, and transmission of stimuli may explain the conjunct nature of so many tissue cells, recent researches on cell lineages may perhaps give us a clue to the interpretation of the fact that blastomeres are in so many cases, no more than coherent. For it is noticeable that wherever cell lineages, with marked isolation of the blastomeres, have been described, there is a decided tendency to the precocious development of organs, or, at any rate, to the precocious isolation of the primordia (Anlage) of organs.

It seems probable that the discrete condition of the blastomeres is connected with the fact, to which I alluded in the earlier part of this essay, that they are, from the very outset, specialised. They have each a definite molecular constitution different from the others, and, in figurative language, a limited part to perform, which they could not perform to advantage if they were conjunct with the other blastomeres and shared in their different molecular constitution. But this is a subject which I must leave for a future occasion when I discuss the validity of von Baer's law of development.

I have travelled in this essay over a great deal of ground, and I have necessarily had to touch more lightly on many topics than I should have wished. I hope that I may at least have succeeded in presenting my arguments in a manner which will make them clear to my readers, and that I have not been too discursive. Starting from Mr. Sedgwick's propositions and accusations, I have tried to show what is or was the exact extent and meaning of the cell-theory; I have tried to examine it and show how much was good and how much bad, and I have finally been led to the conclusion—which is not quite what I proposed to myself at the outset—that the cell concept is a valuable expression of our experience of organic life, both morphologically and physiologically, but that in higher organisms cells are much what von Sachs declares them to be, not independent life units (Lebenseinzelheiten), but a phenomenon so general as to be of the highest significance; they are the constant and definite expression of the formative forces which reside in so high a degree in organic matter.

Lest I should appear to have minimised the importance of the cell too much, let me conclude by saying, that nothing which has appeared above calls into question that great feature of animal and plant development which most impresses the biological student, viz. that organic growth is a cycle, beginning in the single cell, and returning to the single cell again. And therefore, in a limited sense, the cell is par excellence the unit of life. Its growth takes various forms and shows many complexities, but whatever the form, however great the complexity, it is a progress from the state of an independent corpuscle, through a state of many coherent, or continuous, or conjunct, interdependent corpuscles, back again to the state of a single independent corpuscle.

This was the great advance made by Remak on the theory of Schwann, and summed up in Virchow's aphorism, which I believe to be universally true. For Schwann did not hold that cells are the ultimate basis of life: he held that they are formed, as a crystal is formed out of its mother liquor, from a structureless matrix, the cytoblastema. To some such theory Mr. Sedgwick wishes to take us back again, for his "pale and at first sparse reticulum" bears a most suspicious resemblance to the exploded cytoblastema. "The development of nerves," he says, "is not an outgrowth from certain central cells, but is a differentiation of a substance which was already in position." And earlier in his article, referring to the growth and extension of the mesoblast between epiblast and hypoblast, he says: "What are the facts? The space between the layers is never empty. It is always traversed by strands of a pale tissue connecting the various layers, and the growth which does take place between the layers is not a formation of cells but of nuclei, which move away from their place of origin and take up their position in this pale and at first sparse reticulum."

But surely nobody ever affirmed that the space between the layers was empty except in the sense that it is devoid of cellular structures. It is well known that it is filled with a coagulable fluid, and it is worthy of remark that coagulable fluids, treated with the reagents now most in use, frequently form a reticulum of pale non-staining substance. I can speak from experience, for not long since I was much puzzled by such a reticulum, and had I been less cautious I should have published, as a great morphological discovery, statements which rested on a wholly insufficient basis of experience. The subject requires further investigation, and the most that one can say now is, that it is possible that Mr. Sedgwick, good observer as he is, may have been mistaken. And he will pardon my observing that the things which he states are not "facts." They are his own inferences from his own individual observations, and will require very abundant confirmation before they can take rank as what we agree to regard as "facts." All the "facts" we have at present, i. e. the accumulated observations of hundreds of highly-trained and able observers, are fundamentally opposed to any such account of protoplasmic growth apart from nuclear formation as Mr. Sedgwick gives us. But there is another way of looking at it, namely, that he has only overstated his case, and that the growth of the tissues in question resembles the apparent creeping motion of the plasmodia of the Myxomycetes. That this may be the case is supported by a study of Mr. Assheton's recent account of the growth of the mesoblast and of the inner layer of the epiblast in the embryo of the rabbit. It presents no theoretical difficulties, but it should be remarked that Mr. Assheton figures numerous nuclei at the very edge of the growing part of his reticula, which is consonant with what we know of protoplasmic growth in other cases, but not with Mr. Sedgwick's account.

But if Mr. Sedgwick can prove that the reticulum is there and that it grows and spreads far from the nuclei which subsequently migrate into it, he must not suppose, as he is apparently so ready to assume, that the inveterate prejudice of morphologists will prevent their accepting his conclusions because of their theoretical difficulties. If his case is proved, it will be accepted, but he must prove it up to the hilt.

And if he does prove it, what then? It will be an isolated case, of secondary significance: merely another addition to our experience of the very various phenomena displayed in organic growth. For thousands of instances point to the fact that normal growth is effected in a very different way, by mitotic division of the nucleus preceding and directing the formation of a discrete or concrescent cell-corpuscle. The recent researches of cytologists are too many, too good of their kind, and too consistent to admit of any other conclusion.

In Three Volumes, fully Illustrated, royal 8vo, £4 (or separately as below).

A TREATISE ON HYGIENE AND PUBLIC HEALTH.

Edited by THOMAS STEVENSON, M.D., F.R.C.P.,
Lecturer on Chemistry and on Medical Jurisprudence at Guy's Hospital, Official Analyst to the Home Office; and

SHIRLEY F. MURPHY,
Medical Officer of Health of the Administrative County of London, President of the Epidemiological Society.

VOLUME I. Price 28s.

Air. By J. LANE NOTTER, M.A., M.D., Professor of Military Hygiene in the Army Medical School, Netley.

Warming and Ventilation. By W. N. SHAW, F.R.S., Lecturer on Experimental Physics in the University of Cambridge.

Meteorology. By G. J. SYMONDS, F.R.S., Secretary of the Royal Meteorological Society.

Influence of Climate on Health. By C. THEODORE WILLIAMS, M.A., M.D., F.R.C.P., Physician to the Hospital for Consumption and Diseases of the Chest, Brompton.

Water. By THOS. STEVENSON, M.D., F.R.C.P., Lecturer on Chemistry and on Medical Jurisprudence at Guy's Hospital.

The Influence of Soil on Health. By S. MONCKTON COPEMAN, M.A., M.D., D.P.H., Medical Inspector of the Local Government Board.

Food. By SIDNEY MARTIN, M.D., F.R.C.P., F.R.S., Assistant Physician to University College Hospital.

The Inspection of Meat. By E. W. HOPE, M.D., D.Sc., Assistant Medical Officer of Health, Liverpool; Lecturer on Public Health, University College, Liverpool.

Clothing. By GEO. VIVIAN POORE, M.D., F.R.C.P., Physician to the University College Hospital.

Physical Education. By FREDERICK TREVES, F.R.C.S., Surgeon to, and Lecturer on Anatomy at, the London Hospital.

Baths. BY W. HALE WHITE, M.D., F.R.C.P., Physician to Guy's Hospital.

The Dwelling. By P. GORDON SMITH, F.R.I.B.A., Architect to the Local Government Board; and KEITH D. YOUNG, F.R.I.B.A.

Hospital Hygiene. By H. G. HOWSE, M.S., Surgeon to Guy's Hospital.

The Disposal of Refuse. By W. H. CORFIELD, M.A., M.D., Professor of Hygiene and Public Health, University College, London; and LOUIS C. PARKES, M.D., D.P.H., Lecturer on Public Health at St. George's Hospital.

Offensive and Noxious Businesses. By T. WHITESIDE HIME, M.D., late Medical Officer of Health, Bradford.

Slaughter-houses and their Administration. By E. W. HOPE, M.D., D.Sc., Assistant Medical Officer of Health, Liverpool; Lecturer on Public Health, University College, Liverpool.

VOLUME II. Price 32s.

Pathology and Etiology of Infectious Diseases. By E. KLEIN, M.D., F.R.S., Lecturer on General Anatomy and Physiology, St. Bartholomew's Hospital.

Natural History of Infectious Diseases. By T. W. THOMPSON, D.P.H., late Medical Officer of Health to the Herts and Middlesex Combined Sanitary Districts.

Vital Statistics. By ARTHUR RANSOME, M.D., F.R.S., Examiner in Public Health in Cambridge University.

Marine Hygiene. By H. E. ARMSTRONG, D.Hy., Medical Officer of Health of Newcastle-upon-Tyne and the River Tyne Port.

Smallpox and Vaccination. By JOHN MCVAIL, M.D., F.R.S.E., Medical Officer of Health of the Counties of Stirling and Dumbarton.

Military Hygiene. By J. LANE NOTTER, M.D., Professor of Military Hygiene at the Army Medical School, Netley.

Disposal of the Dead. I. By Sir T. SPENCER WELLS, Bart., F.R.C.S.Eng. II. By FREDK. WALTER LOWNDES, Surgeon to the Liverpool Police.

The Medical Officer of Health. By ALFRED ASHBY, M.B., F.R.C.S., Medical Officer of Health of Reading.

VOLUME III. Price 20s.

THE PUBLIC HEALTH LAW OF ENGLAND, IRELAND, AND SCOTLAND.

*** *Though for Departmental reasons the names of the Writers in the Third Volume do not appear, the Editors desire to state that each of its Articles is by a Gentleman of recognised legal ability, officially engaged in the administration of the law of that part of the United Kingdom to which his Article relates.*

LONDON: J. & A. CHURCHILL, 11, NEW BURLINGTON STREET.

with the regards of
Chas. B. Davenport.

Proceedings of the American Academy of Arts and Sciences.

Vol. XXXII. No. 4. — December, 1896.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, E. L. MARK, DIRECTOR, No. LXXIII.

STUDIES IN MORPHOGENESIS, VI.

A CONTRIBUTION TO THE QUANTITATIVE STUDY OF CORRELATED VARIATION AND THE COMPARATIVE VARIABILITY OF THE SEXES.

By C. B. Davenport and C. Bullard.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, E. L. MARK, DIRECTOR, No. LXXIII.

STUDIES IN MORPHOGENESIS, VI.

A CONTRIBUTION TO THE QUANTITATIVE STUDY OF CORRELATED VARIATION AND THE COMPARATIVE VARIABILITY OF THE SEXES.

By C. B. Davenport and C. Bullard.

Presented October 14, 1896.

The following quantitative study of variation is based upon counts of the Müllerian glands of the fore legs of 4,000 swine. Our attention was directed to these glands as favorable objects of study by Gertrude Crotty Davenport, who had already collected some data concerning their variability. These data, together with valuable suggestions derived from her own experience, she generously placed at our disposal.

The positions of the Müllerian glands are indicated upon the wrist by large openings or pits, about 1 mm. in diameter, which are found only upon the inner aspect of the fore legs. The number of pits is variable. Where there are several they occur, for the most part, in a single row trending somewhat obliquely to the long axis of the leg.

Of the 8,000 legs examined, the arrangement of the glands was studied on only 2,000 legs, 1,000 male and 1,000 female. The total number of glands on a single leg varies from 0 to 10. When the number is large, some of the glands are frequently found outside the main row. In no case have we found more than nine glands in one row. We may call those lying outside the main row *lateral* glands. The lateral glands usually (six exceptions) occur at the upper (proximal) end of the series. Their number does not usually exceed two, but in a single case we have found four. These four glands lay in a secondary row parallel to the main row, which contained five glands. In one other case, where three lateral glands were found, these lay parallel to the main row of five. When there are two glands they may lie either in a line parallel with the main row, or make any angle up to 90° with it. Lateral glands occur more rarely when the total number of glands on the leg is small, but we have found one extreme case in which the only two glands on the leg occurred side by side, i. e. in a transverse row.

The reduction in the number of glands takes place from one end, — the distal end of the series. Generally, where there are only two or three glands these occur high up and the normal diatance apart. Rarely, however, the reduction is brought about in part by the failure to develop in the middle of the series while glands develop near the extremes, so that there is a broad hiatus in the series.

Since the proximal end of the series is that at which glands are most likely to be formed, and since they tend to be produced more abundantly there, this end, which occupies the region of the upper wrist, is to be considered as the source of the morphogenic impulses which give rise to the glands. Sometimes the embryonic Anlage does not develop beyond this point; sometimes, on the other hand, it develops along the whole extent of the wrist in one row, and even forms an accessory "lateral" row.

The total number of swine examined was, as stated, 4,000; of which 2,000 were males and 2,000 females. The total number of fore legs examined was, accordingly, 8,000; 4,000 left and 4,000 right. All of the observations fall, consequently, into four groups of 2,000 cases each; namely, male right, male left, female right, female left. These four groups will be considered, for the most part, separately.

We first determined how many legs in each of these classes had no glands, one gland, two glands, and so on. The results are given in the following table.

TABLE I.

No. of Glands.	0	1	2	3	4	5	6	7	8	9	10	Total.
♂ R	15	225	353	437	411	297	155	78	16	12	1	2,000
♂ L	14	241	336	430	429	295	159	53	30	10	3	2,000
Total ♂	29	466	689	867	840	592	314	131	46	22	4	4,000
♀ R	15	209	365	482	414	277	134	72	22	8	2	2,000
♀ L	21	213	361	438	432	288	149	69	16	11	2	2,000
Total ♀	36	422	726	920	846	565	283	141	38	19	4	4,000
Total ♂ + ♀	65	888	1415	1787	1686	1157	597	272	84	41	8	8,000

In the following table, which is based upon the preceding, the numbers are all reduced to per milles. The two lines of totals are here, accordingly, replaced by means. A glance at this table shows a close parallelism between the distribution of glands in the four cases.

TABLE II.

Summary per Mille.

No. of Glands.	0	1	2	3	4	5	6	7	8	9	10
♂ R	7.5	112.5	176.5	218.5	205.5	148.5	77.5	39.0	8.0	6.0	0.5
♂ L	7.0	120.5	168.0	215.0	214.5	147.5	79.5	26.5	15.0	5.0	1.5
Mean ♂	7.2	116.5	172.2	216.8	210.0	148.0	78.5	82.8	11.5	5.5	1.0
♀ R	7.5	104.5	182.5	241.0	207.0	138.5	67.0	36.0	11.0	4.0	1.0
♀ L	10.5	106.5	180.5	219.0	216.0	144.0	74.5	34.5	8.0	5.5	1.0
Mean ♀	9.0	105.5	181.5	230.0	211.5	141.3	70.7	35.2	9.5	4.7	1.0
Mean of ♂ and ♀	8.1	111.0	176.8	223.4	210.7	144.7	74.6	34.0	10.5	5.1	1.0

Several interesting questions now arise:

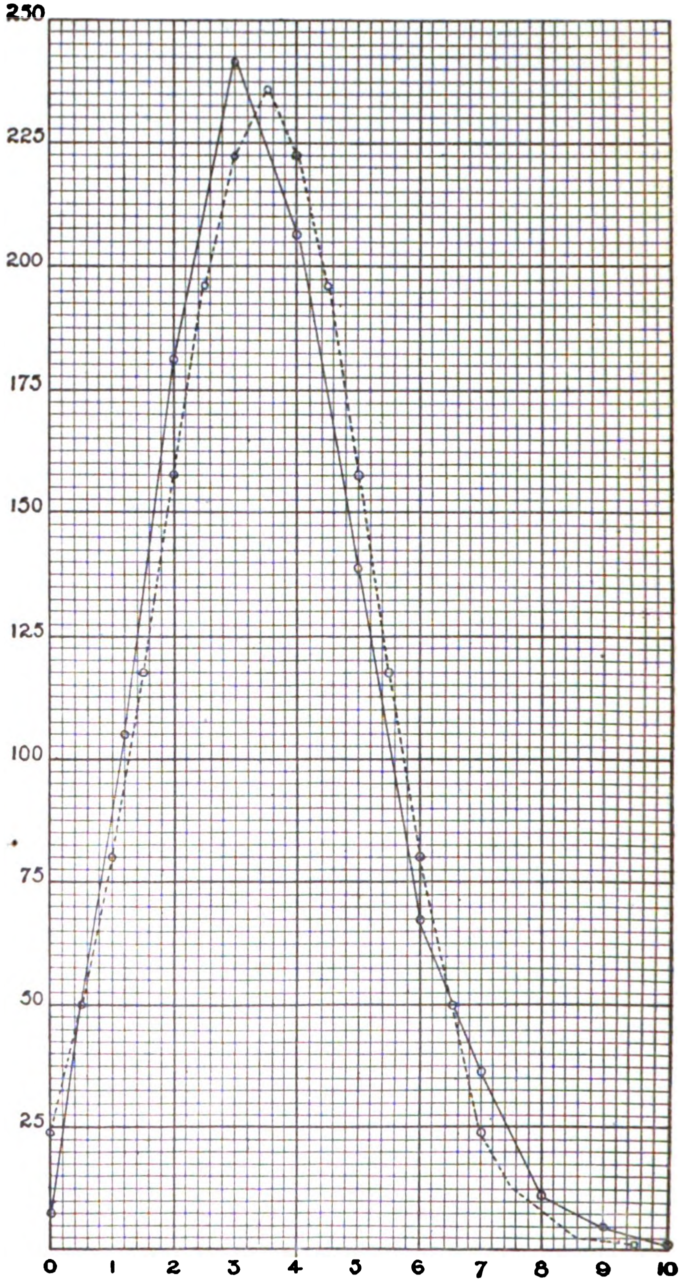
(1) How closely similar is the average number of glands in the two sexes, and in the right and left leg of the same sex?

(2) Which sex shows the greater variability, and to what extent is it greater? Is the relation between the variability of the right and left legs closer than that between the two sexes?

(3) How closely correlated are the numbers of glands on the right and left legs of individuals? That is to say, what are the chances that a swine which has 2, 4, or 7 glands on the right leg will have the same number on the left leg also?

1. *The Relation between the Abundance of Glands and the Sex or the Side of the Body.*

The average number of glands on a leg of either sex is determined by dividing the total number of glands counted in that leg by the number of individuals of that sex, in this investigation 2,000. This gives us the following result: —


250
225
200
175
150
125
100
75
50
25
0
1
2
3
4
5
6
7
8
9
10

1.	Average number of glands in	♂	R	. . . .	3.547
2.	" " "	♂	L	. . . .	3.540
3.	" " "	♀	R	. . . .	3.501
4.	" " "	♀	L	. . . .	3.521

Comparing the average of (1) and (2) with the average of (3) and (4) it appears that the average number of glands in the males (3.544) is tolerably close to that in the females (3.511) but that a real difference exists between the two. *The glands are slightly less abundant in the female than in the male in the ratio*, 100 : 100.94. The average number of glands on the right side of the body is so close to that on the left side (3.524 : 3.531) that we may conclude: *The average numbers of the glands on the right leg and on the left leg taken without regard to sex are about equal.*

2. *Variability correlated with the Sex and with the Side of the Body.*

In seeking to determine whether, in this matter of glands, male or female swine are the more variable, it is necessary to employ a method of stating variability quantitatively. Quetelet, Stieda, and Galton* have employed such a method, based upon the fact that the organs of an animal vary about their mean dimensions to an extent and with a frequency indicated by the probability-of-error equation,†

$$y = k \,.\, e^{-h^2x^2}.$$

Two of the principal features involved in such a distribution are that deviations of a given size are equally apt to occur above and below the mean, and that small deviations are more apt to occur than large ones. These and other characters of the "probability" curve are indicated in that shown in dotted line in the accompanying diagram. The diagram also shows the curve of distribution of the various numbers of glands occurring on a leg, from 1 to 10. This curve is drawn from the right female leg only; the curve for the other legs would be very similar. We shall speak in a moment of the method of construction of these curves; but we want now to call attention to the fairly close similarity of the two curves, — that gained by observation and the theoretical one, — a similarity so close that we are justified in concluding that the law of distribution of the variants in the leg glands of swine is the same as that of accidental errors.

* Quetelet, Lettres sur la théorie des probabilités, Bruxelles, 1846. Stieda, in Archiv für Anthropologie, Bd. XIV. pp. 167–182. Galton, Natural Inheritance, New York and London, 1889.

† See any text-book on "Least Squares."

This being granted, we can express quantitatively the degree of variation in the glands by determining the *average deviation* in the number of glands of any set of legs from the mean number of that set. Thus in the right leg of the female the mean number of glands is approximately 3.5. Since there is no individual with 3.5 glands on the leg, every individual shows in the number of its leg glands a departure of at least 0.5 from the mean. Adding together the departures of every individual and dividing by the total number of individuals (2,000) we get the mean departure, which is known to mathematicians as the mean error, and is indicated by the formula $\frac{\Sigma x}{n}$, in which Σx indicates the *sum* of the individual departures, x, and n the total number of individuals. Proceeding in this way, the average departure, as an *Index of Variability*, was determined to be as follows for each set of legs: —

Average departure of	♂ R	1.41089
" " "	♂ L	1.41083
" " "	♀ R	1.36457
" " "	♀ L	1.38766

These determinations indicate that the variability of the right and the left legs, of the male is exactly the same to four places of decimals; that the variability of the right leg of the female is slightly less than that of the left leg, and that the male shows a greater variability than the female in the ratio of about 1.411 : 1.376, or 1.025 : 1.000. In other words, the male is 2.5% more variable than the female.

As we have seen, the variabilities of the right and of the left sides of the male are practically equal. In the female, the left side is more variable. Disregarding sex, we find the variability of the left side is to that of the right as 1.3993 : 1.3877, or as 1.0084 : 1. That is to say, the glands are 0.8% more variable on the left side than on the right.

Let us now compare the relative variability of symmetrical legs with that of the two sexes. We find the variability to be greater between the same leg (say the right) in opposite sexes, than between symmetrical legs. The relation may be expressed by the ratio 1.025 : 1.0084, or 1.016 : 1. These numbers indicate a closer morphogenetic kinship between the two legs of a symmetrical pair than between the corresponding leg in different sexes.

We may now briefly indicate the method of constructing the probability curve in the diagram. The abscissas represent the numbers of glands from 0 to 10 on a leg, and the ordinates the corresponding number of individuals per mille. The mean number of glands is 3.50 and the index of variability is 1.3646. With these data, we can draw a probability curve including about the same area as our observed curve. This curve, the continuous line, is drawn from the equation

$$y = k \, . \, e^{-h^2 x^2}.$$

h is the so called index of precision, and is equal to the reciprocal of the index of variability divided by the square root of π, thus,

$$h = \frac{n}{\Sigma x \sqrt{\pi}}.$$

e is the base of the Napierian system of logarithms; namely, 2.1718.

k is a constant determined by multiplying the quotient of $\frac{h}{\sqrt{\pi}}$ by the interval (dx) between successive values of x, in this case, 1; thus,

$$k = \frac{h\,dx}{\sqrt{\pi}}.$$

x indicates deviations from the mean value, and y the corresponding ordinates.

When $x = 0$, $y = k$, which is thus the length of the ordinate at the mean value of x. Its value gives the percentage of cases which should theoretically occur at the mean; it is in this case 23.3%. Like h, k might be taken as a measure of precision, since it increases as variability diminishes.

3. *The Degree of Correlation between the Number of Glands on the Right and the Left Legs of Individuals.*

To get quantitative results in this matter we must employ a method devised by Galton.* This method depends upon the following procedure and considerations. Separate the right legs into as many lots as there are degrees of deviation from the mean number of glands. These lots may be called the subjects. Find for each of the subjects the mean deviation in the number of glands on the left legs of the corresponding individuals (the relative). The deviation of any subject and the deviation of the corresponding relative are to be compared. In order to make this comparison instructive, we must take into account the fact that left legs (for example) are more variable than right legs. In order to eliminate this

* Galton's method is explained in his paper in the Proc. Roy. Soc., Vol. XLV. p. 135, 1889.

difference, divide the deviation of the subjects by their index of variability and the deviation of the corresponding relatives by their index of variability. If now, the correlation is perfect, those causes which have produced a deviation from the mean in the right leg will act in precisely the same degree on the left leg also, and thus the deviation of any relative will not differ from the deviation of the corresponding subject. If, under these circumstances, we divide the mean deviation of the relatives by that of the subjects, the quotients will average 1. This average quotient is called the Index of Correlation. Thus, the index of perfect correlation is 1.

Let us suppose, on the contrary, that there is no correlation whatever between the number of glands in any subject and in the corresponding relative, then, no matter what the number of glands in any subject, the number in the corresponding relative is just as apt to be large as small, and will be equal to the average number of glands in the whole group; in other words, no matter what the deviation of the subject is, that of the relative will be 0. The average quotient obtained, under these circumstances, by dividing the deviation of relatives by the deviation of the subjects, will consequently always be 0. Thus the index of entire lack of correlation is 0.

An inverse correlation, in which a positive deviation of the subject from the mean shall always be accompanied by a negative deviation of the relative, will be represented by a minus quantity. Thus the correlation of any two sets of compared organs will lie between $+1$ and -1. The size of the fractions lying between ± 1 and 0 will serve to indicate the degree of correlation.

The quotient, r, obtained by dividing the deviation (always in units of the average deviation) of the left legs by that of the corresponding right will not be the same for all the lots of individuals. The true index of correlation, R, will be found by taking the average of all the ratios, r, r', r'', r''', etc. This process of finding R may be somewhat abbreviated from the following considerations. We have seen that

$$r = \frac{\dfrac{\text{Deviat. of Rel.}}{\text{Avg. Dept. of Rel.}}}{\dfrac{\text{Deviat. of Subj.}}{\text{Avg. Dept. of Subj.}}} = \frac{\dfrac{d_r}{A_r}}{\dfrac{d_s}{A_s}};$$

also that

$$R = \frac{1}{n}\left(r + r' + r'' + \ldots . r^n\right) = \frac{1}{n}\Sigma r;$$

consequently,

$$R = \frac{1}{n}\left(\frac{\frac{d_r}{A_r}}{\frac{d_s}{A_s}} + \frac{\frac{d'_r}{A_r}}{\frac{d'_s}{A_s}} + \frac{\frac{d''_r}{A_r}}{\frac{d''_s}{A_s}} + \dots \frac{\frac{d^n_r}{A_r}}{\frac{d^n_s}{A_s}}\right) = \frac{1}{n}\Sigma\frac{\frac{d_r}{A_r}}{\frac{d_s}{A_s}} = \frac{A_s}{A_r}\cdot\frac{1}{n}\cdot\Sigma\frac{d_r}{d_s},$$

since A_s and A_r are constant. It results from this that it is only necessary to find the mean of the ratios of the untransmuted deviations and multiply this by the quotient $\frac{A_s}{A_r}$. This saves a great many divisions, and it has been the method pursued in our work.

After this statement of the method of expressing correlation we now pass to a consideration of the results obtained with the glands of the pig. We shall consider first the correlation between the number of glands on the right leg of the male with that on the left leg of the male.

TABLE III.

♂ R CORRELATED WITH ♂ L.

Relatives. Subjects.	0l	1l	2l	3l	4l	5l	6l	7l	8l	9l	10l	No. of Indivs. Right leg.	Means of Lefts.	Dev. of Rel. (d_r)	Dev. of Sub. (d_s)	Quo. $\frac{d_r}{d_s}$
0r	8	5	2	—	—	—	—	—	—	—	—	15	0.600	−2.940	−3.547	.829
1r	4	151	58	9	3	—	—	—	—	—	—	225	1.360	−2.180	−2.547	.856
2r	2	65	154	96	28	7	1	—	—	—	—	358	2.306	−1.234	−1 547	.798
3r	—	14	88	173	128	28	6	—	—	—	—	437	3.197	−0.343	−0.547	.627
4r	—	5	27	119	153	77	26	3	1	—	—	411	3.888	+0.348	+0.458	.768
5r	—	1	7	24	92	101	52	11	9	—	—	297	4.784	+1.244	+1.453	.856
6r	—	—	—	8	16	58	48	16	7	0	2	155	5.510	+1.970	+2.453	.803
7r	—	—	—	1	8	20	18	17	9	5	—	78	6.141	+2.601	+3.453	.753
8r	—	—	—	—	1	3	5	3	2	2	—	16	6.500	+2.960	+4.453	.665
9r	—	—	—	—	—	1	3	3	2	2	1	12	7.333	+3.793	+5.453	.696
10r	—	—	—	—	—	—	—	—	—	1	—	1	9.000	+5.460	+6.453	.846
No. of Indivs. Left Leg.	14	241	336	430	429	295	159	53	30	10	3	2,000	Mean,			.772

In this table the first column names the subjects, of which there are as many as there are numbers of glands, viz. 0 to 10. In the succeeding columns on a single line is exhibited the distribution of the number of glands on the corresponding left legs. The column headed "Means of Lefts" gives the average number of glands on the left legs of the individuals which make up the corresponding subject. The column headed "Deviation of Rel. (d_r)" gives the deviations of the corresponding "Means of Lefts" from the mean number of left male glands. The column "Dev. of Subject (d_s)" gives the deviation of the subjects from their mean number. The last column is the quotient of d_r divided by d_s. This gives r, r', r'', etc. The last number in the column is the mean of all these values of r. This number multiplied by $\frac{A_s}{A_r}$ will give R, the value sought. But $\frac{A_s}{A_r}\left(=\frac{1.41083}{1.41089}\right)$ is nearly unity, so that the Index of Correlation of the number of glands of the right and left legs is .772. Galton has shown that the same ratio holds true when relative and subject are interchanged.

By a process similar to the preceding we have found that the ratio of correlation of right and left legs in the female is .783. This ratio is so similar to that obtained for males as to justify the conclusion that *the index of correlation in variability of the leg glands is approximately equal in the two sexes, and is about* .777.

The conclusions from this study may now be summed up. We have in the leg glands of swine a serially arranged system of organs developing, for the most part, in one line, starting at one point, and extending out a variable distance. On such a system of organs we investigate quantitatively the question, How closely similar are the morphogenic processes which determine the resemblance of these glands on the opposite sides of the body and in the two sexes? First of all, the *average* number of glands is tolerably but not strikingly close on the two fore legs and in the two sexes. The glands are nearly 1% more abundant in the male than in the female. When we come to study their variability we find that the variants are distributed in accordance with the probability curve, very nearly. (See diagram.) A curious lack of symmetry results from the fact that, since the mean lies at 3.5, variation is limited to 3.5 in one direction, but is unlimited (reaches as a matter of fact to 6.5) in the other. The degree of variability in the right and left legs is, especially in the case of the male, strikingly similar, being 1.41089 and 1.41083 in the two cases respectively, the difference being within the errors of the method. The males are about 2.5% more variable than the females. The glands are 0.8% more variable on the left side than on the right. The relative variability of the same leg in the different sexes is about 1.6% greater than that of the two legs in the same sex. The degree of correlation in the variability of the right and left legs is about .777.

CAMBRIDGE, MASS., July 25, 1896.

PUBLICATIONS

OF THE

AMERICAN ACADEMY OF ARTS AND SCIENCES.

MEMOIRS. Old Series, Vols. I.–IV.; New Series, Vols. I.–XI. 15 volumes, $10 each. Half volumes, $5 each. 25% discount to booksellers; 50% to members.

Vol. X.	Part II. *bis*			$1.75
" XI.	" I.			2.00
" XI.	" II.	No. I.		3.00
" XI.	" III.	" II.–III.		1.00
" XI.	" IV.	" IV.		1.00
" XI.	" IV.	" V.		.75
" XI.	" V.	" VI.		.25
" XI.	" VI.	" VII.		2.00
" XII.	No. I.			1.50

PROCEEDINGS. Vols. I.–XXXI., $5 each. 25% discount to booksellers; 50% discount to members.

Complete sets of the Memoirs, 15 vols., for $112.50, to members, $60; of the Proceedings, 31 vols. for $116.25, to members, $62.

From the PROCEEDINGS OF THE ROYAL SOCIETY, VOL. 57.

6

REPORT OF THE COMMITTEE, CONSISTING OF MR. GALTON (CHAIRMAN), MR. F. DARWIN, PROF. MACALISTER, PROF. MELDOLA, PROF. POULTON, AND PROF. WELDON, "FOR CONDUCTING STATISTICAL INQUIRIES INTO THE MEASURABLE CHARACTERISTICS OF PLANTS AND ANIMALS."

PART I.—AN ATTEMPT TO MEASURE THE DEATH-RATE DUE TO THE SELECTIVE DESTRUCTION OF *CARCINUS MÆNAS* WITH RESPECT TO A PARTICULAR DIMENSION.

BY

PROF. WELDON, F.R.S.

[*From the* PROCEEDINGS OF THE ROYAL SOCIETY, VOL. 57.]

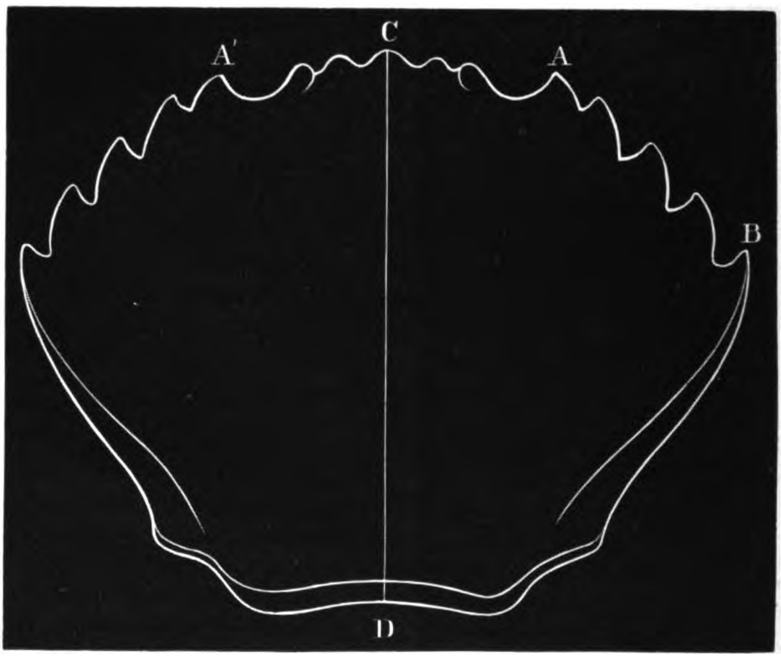
Report of the Committee, consisting of Mr. Galton (Chairman), Mr. F. Darwin, Professor Macalister, Professor Meldola, Professor Poulton, and Professor Weldon, "for Conducting Statistical Inquiries into the Measurable Characteristics of Plants and Animals." Part I. "An Attempt to Measure the Death-rate due to the Selective Destruction of *Carcinus Mænas* with respect to a Particular Dimension."—Drawn up for the Committee by Professor WELDON, F.R.S. Received November 20, 1894.

Among the material available for the purposes of the Committee was a sample of *Carcinus mænas*, from Plymouth Sound, including a fairly large number of young females. The distribution of abnormalities in certain dimensions had already been determined for adult females from the same locality ('Roy. Soc. Proc.,' vol. 54, pp. 318—329); and it seemed worth while to compare the frequency of abnormalities in young individuals at various stages of growth with the frequency of the same abnormalities in adult life, so as to determine whether any evidence of selective destruction during growth could be discovered or not.

About 7000 females, varying in length from 7·00 to 13·95 mm., were chosen (at random, except as regards their size), and two dimensions were measured in each. The results were then compared with those of the corresponding measurements, made upon a sample of 1000 adult females from the same locality, which are recorded in the paper just referred to.

The dimensions chosen were:—(1) the "*frontal breadth*"—the distance in a straight line between the tips of the extra-orbital teeth of the carapace (from the point A, fig. 1, to the corresponding point on the opposite side); and (2) the "*right dentary margin*," measured in a straight line from the apex of the first to that of the last lateral tooth (from A to B, fig. 1). The "length" of each crab was taken as the length of the carapace, from the tip of the middle inter-orbital tooth to the posterior margin (from C to D, fig. 1). This is, of course, not the total length of the body; but the curvature and flexibility of the abdomen render an exact determination of the real body length very difficult.

Fig. 1.



In order to compare the variability of a dimension in crabs whose carapace is only 7 mm. long with that of the corresponding dimension in adult crabs, whose carapace length is from 40—50 mm. or more, it is evidently necessary to adopt some method of picturing the crabs as of one standard size; and accordingly the measures obtained have always been expressed in terms of the carapace-length of the crab to which they belong, taken as 1000. The measurements were made by means of a screw, of 1 mm. pitch, carrying the object across the field of a microscope, and by means of graduations on the head of the screw the observations were recorded to the nearest hundredth of a millimetre. It is believed that the probable error of any observation is not much more than one hundredth of a millimetre. In order to minimise the effect of errors of observation, the results, after being expressed as fractions of the carapace-length, were sorted into groups, such that the measures in each group did not differ by more than 0·004 of the carapace-length, and all measures in the same group were treated as identical. The unit employed in tabulating the results was therefore 0·004 of the carapace-length; but in what follows the results are expressed, for the greater convenience of the reader, in thousandths of the carapace-length. It will be noticed that the principal effect of this alteration upon the results is to diminish their apparent regularity—an aberration of one unit of measurement appearing as four units in the tables below.

1. *Variation in Frontal Breadth.*

An initial difficulty in determining the error of distribution of frontal breadths about their mean in young crabs, arises from the great rapidity with which the mean itself changes during growth. The mean frontal breadth in the smallest specimens was found to be 853·14 thousandths of the carapace-length, while at maturity it is only 604·94 thousandths. The rate at which this change occurs can be gathered from the following table of the crabs measured, and the same result is graphically shown in fig. 2

From this table it appears that the mean frontal breadth changes at such a rate that when the carapace-length has increased 0·2 mm., the frontal breadth has almost always diminished by less than four thousandths, that is to say, by less than one of the units of measurement here employed. For the purpose of the present investigation the mean was therefore considered stationary during every period of increase in size of not more than 0·2 mm., and the young crabs were accordingly sorted into groups, the individuals of each group differing by less than 0·2 mm. in respect of their carapace-length. The distribution of frontal breadths about the mean was then examined in each group separately.

As the difference in size between the largest and the smallest of the growing crabs was 7 mm., it follows that the material was divided into thirty-five groups. This subdivision of the material had great disadvantages, because, instead of a single group of over 7000 individuals, varying about the same mean, from which a fairly reliable indication of the law governing frequency of deviation might have been expected, the average number of individuals in any one of the available groups was only 200; and from so small a number of obser-

Table I.—Mean Frontal Breadth (F) expressed in thousandths of the Carapace-length, corresponding to various Carapace-lengths (C), together with the Number of Individuals on which each Determination is based.

C.	F.	Number.	C.	F.	Number.
7·1	853·14	159	10·7	798·01	225
7·3	852·43	186	10·9	794·96	162
7·5	850·89	172	11·1	792·14	222
7·7	844·27	142	11·3	789·26	218
7·9	844·22	132	11·5	789·26	230
8·1	837·13	224	11·7	786·07	211
8·3	835·41	219	11·9	784·53	225
8·5	830·08	214	12·1	782·42	224
8·7	826·80	207	12·3	780·92	226
8·9	823·75	214	12·5	778·39	219
9·1	821·26	191	12·7	772·76	183
9·3	818·33	205	12·9	771·62	233
9·5	815·89	214	13·1	770·36	131
9·7	811·60	195	13·3	769·86	162
9·9	809·95	226	13·5	767·70	158
10·1	809·27	245	13·7	762·51	201
10·3	803·21	253	13·9	763·47	211
10·5	800·53	232	(Adult)	(604·94)	(998)

[*Note.*—The carapace-length given in the table is the mean of all lengths included in each group. For example, the entry 7·1 includes all crabs measured in which the carapace-length was between 7·00 mm. and 7·19 mm., and so on.]

vations no satisfactory demonstration of the law of variation at any given moment of growth could be obtained. Nevertheless it was necessary, before proceeding further, to ascertain with some certainty what the law of variation through the whole series really was. The belief in which the work was undertaken was, that the law of variation would be found throughout to be that of the ordinary probability equation ; and this belief was tested in the following way :—In each of the thirty-five groups, the arithmetic mean of the frontal breadths, and the mean of all the deviations from it, were determined; and from the "mean error" found in this way the modulus of the probability function was calculated. Then, by calling the mean of each group zero, and expressing the deviations from the mean in terms of the modulus, a number of curves were obtained, in each of which the modulus was unity and the mean zero; a similar curve of adults was constructed, and the corresponding ordinates of all the thirty-six curves so obtained were added together. It is evident that, if the chance function really expresses the law of variation throughout the series, then the curve resulting from the treatment described will be a symmetrical probability curve of unit modulus. The actual

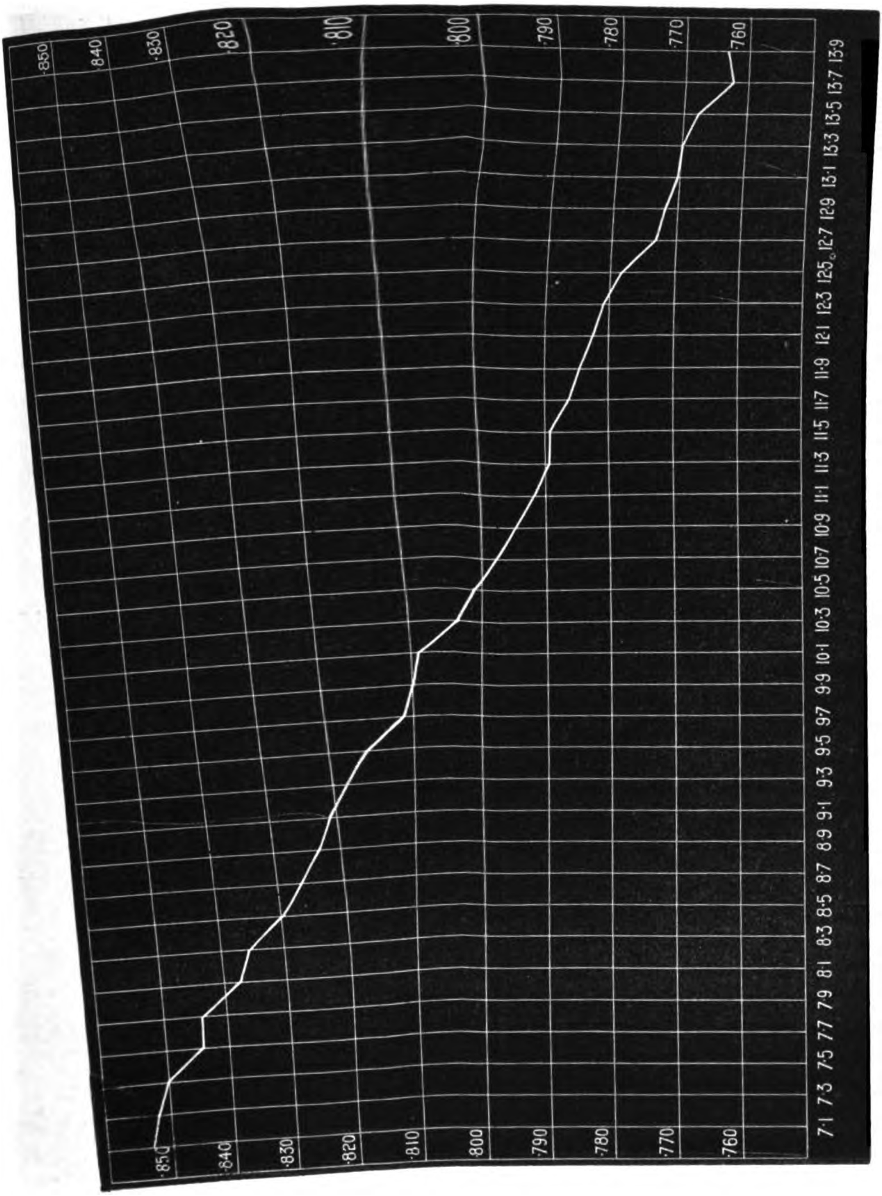


FIG. 2.—Diagram to illustrate the Change in the Mean Value of the Frontal Breadth with Growth in Carapace-length. Ordinates represent fractions of the Carapace-length. Abscissæ represent Carapace-length in millimetres.

curve obtained is plotted in Fig. 3, and the frequency of occurrence of every observed deviation is compared with that indicated by the tables of the probability integral in Table II. In spite of some discrepancies, the general agreement between the observed frequency of

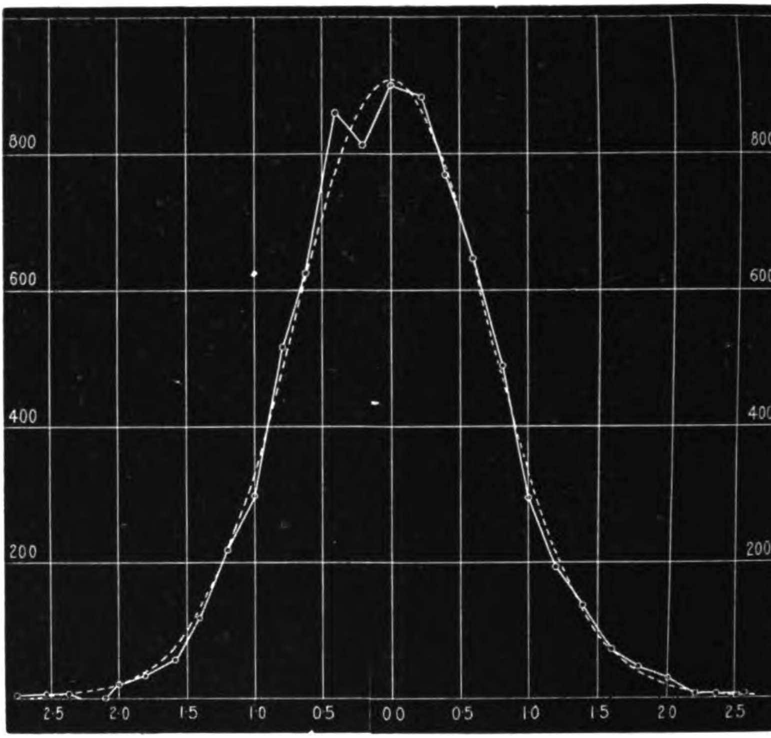


Fig. 3.—Distribution of Frontal Breadths in 8069 Female Crabs from Plymouth Sound, old and young. Deviations expressed in terms of the Modulus. The three cases of deviation greater than three times the Modulus are omitted.

deviations and that indicated by the probability integral is fairly close. The mean error of the observed curve is 0·5621, whereas it should be $1/\sqrt{\pi} = 0{\cdot}5642$, the difference between the two figures being less than 0·5 per cent. The error of mean square is 0·7123, instead of 0·7071, a difference of less than 1 per cent. The sum of the squares of the positive deviations is 2115. The sum of the negative deviations is 1992. The total number of individuals of deviation more than 0·1 is 3593 on the positive, 3574 on the negative side, a difference of about one-half per cent.

On the whole it may be said that the result agrees with that given by the theory of probability as well as could be expected from the number of observations, and that the law of frequency of variation throughout the series may, as was hoped, be assumed to agree with the ordinary law of chance.

From the result so far obtained it followed that a determination of the quartile deviation, or any other of the constants of the pro-

Table II.—Frequency of all Observed Deviations from the Mean Frontal Breadth in 8069 Female Crabs, young and adult, from Plymouth. The Deviations expressed in terms of the Modulus.

Limits of deviations.	Mean deviation.	Observed frequency.	Theoretical frequency.
Over +3·29	+4·790	2	
From +3·10 to 3·29	+3·280	1	
„ +2·90 „ 3·09	—	0	
„ +2·70 „ 2·88	+2·880	1	12
„ +2·50 „ 2·69	+2·575	4	
„ +2·30 „ 2·49	+2·355	4	
„ +2·10 „ 2·29	+2·207	4	
„ +1·90 „ 2·09	+2·003	28	17
„ +1·70 „ 1·89	+1·788	46	36
„ +1·50 „ 1·69	+1·598	71	71
„ +1·30 „ 1·49	+1·395	137	129
„ +1·10 „ 1·29	+1·205	194	217
„ +0·90 „ 1·09	+1·006	295	336
„ +0·70 „ 0·89	+0·805	492	481
„ +0·50 „ 0·69	+0·589	649	635
„ +0·30 „ 0·49	+0·391	769	774
„ +0·10 „ 0·29	+0·191	896	872
„ +0·09 „ −0·09	−0·011	902	907
„ −0·10 „ 0·29	−0·213	814	872
„ −0·30 „ 0·49	−0·404	862	774
„ −0·50 „ 0·69	−0·611	626	635
„ −0·70 „ 0·89	−0·806	517	481
„ −0·90 „ 1·09	−1·000	299	336
„ −1·10 „ 1·29	−1·194	219	217
„ −1·30 „ 1·49	−1·403	118	129
„ −1·50 „ 1·69	−1·589	58	71
„ −1·70 „ 1·89	−1·808	33	36
„ −1·90 „ 2·09	−2·016	18	17
„ −2·10 „ 2·29	−2·210	1	
„ −2·30 „ 2·49	−2·368	4	
„ −2·50 „ 2·69	−2·520	3	12
„ −2·70 „ 2·89	−2·750	1	
—	—	—	
Over	−4·450	1	

bability equation, would be a trustworthy guide to the frequency of abnormalities at various periods of growth. But just as the individual groups were too small to allow of a determination of the law of abnormality in each, so they were too small to give trustworthy values of the quartile. The quartile deviation changes so slowly with growth, that it may without serious error be assumed to be constant during the period represented by 1 mm. of growth in carapace-length: that is, through the period covered by five of the groups into which the growing crabs were sorted. Therefore, after the quartile deviation had been determined in every group, the results were arranged in fives, and the mean of every consecutive five was taken as the quartile deviation through 1 mm. of growth. The results are shown in Table III.

Table III.—Quartile Deviation of Frontal Breadths (Q) for various Magnitudes of Carapace-length (C).

C.	Mean Q.
7·5	9·42
8·5	9·83*
9·5	9·51
10·5	9·58
11·5	10·25
12·5	10·79
13·5	10·09
(Adult)	(9·96)

The values here given are probably not very reliable, but they show that in the youngest individuals the quartile deviation is distinctly less than at maturity; that it increases with increase of size, until a time arrives when it is distinctly greater than in adult life; and that finally it diminishes again.

The initial features of this result,—the smallness of the quartile error at a young age, indicating relative infrequency of deviations, and the increase during growth, have been observed by Bowditch in the case of human stature. The result obtained by Dr. Bowditch and that here described are both simply confirmations of Darwin's statement, that many variations appear at a late period of development.

The initial increase in the quartile error may be attributed to the fact that average young produce upon the whole average adults, while animals which exhibit a deviation of known amount in the young state, exhibit on the whole a greater deviation with advancing age. If this view be the true one (and it is hoped that next year it may be possible to test it by observation of living crabs, which can be measured at various periods of growth), then, in a Plymouth crab, which is of unit deviation when its carapace is 7 mm. long, the most probable deviation when it has grown to be 12·5 mm. in length will be 10·79/9·42 = about 1·15 units. The probable error of this expectation is the expression of irregularities in the rate of growth, which cannot at present, for want of knowledge, be adequately discussed.

From the age represented by a length of 12·5 mm., the quartile

* Of the four very abnormal values shown in the table, three occurred in this group. They have been omitted in the determination of the quartile deviation, which would otherwise become 9·92.

error diminishes, and the parallel between the behaviour of the frontal breadth in Plymouth crabs and that seen by Bowditch in the stature of civilised human beings ceases to hold. The obvious suggestion by which to account for this seems to be that in the United States, where Bowditch made his observations, human beings are under conditions of such civilisation that there is considerable protection of the physically unfit; and that here, as in other civilised countries, any influences which might in a savage race produce selective destruction are reduced to a minimum, whereas in the case of the crabs such selective influences are active.

It is, of course, possible that the deviation of "abnormal" young may in each individual case first attain a maximum and then diminish with advancing age; if this is the case, we cannot know without experiment. In the absence of such experiment, the hypothesis may be provisionally adopted that the diminution in the frequency of individuals of given deviation is due to a selective destruction, and the consequences of this hypothesis will be examined.

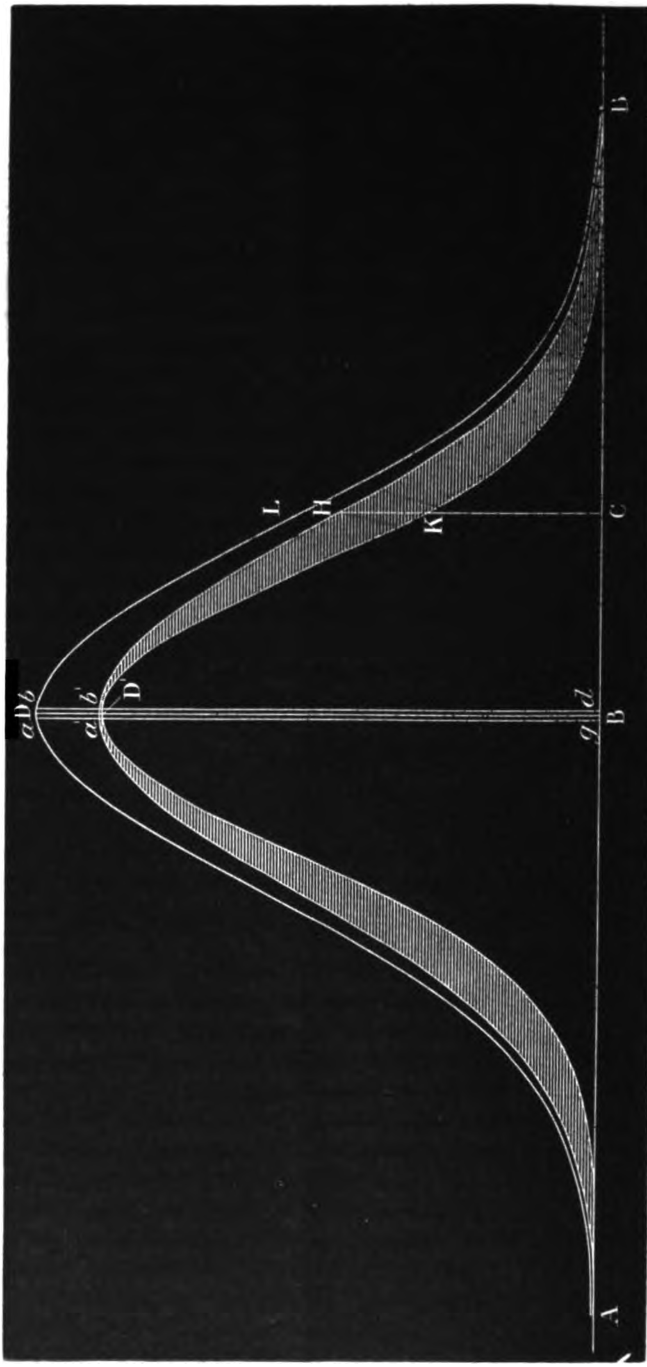
Consider a population of crabs, measured at the time of their maximum variability, and suppose the distribution of deviations among the population to be accurately represented, for a particular organ, by a probability equation of modulus c_1. Now, let the number of individuals of deviation lying between $\pm\, a$ be represented by the area *abgd* (fig. 4); then, if $gd = 2a$ be small, compared with the observed range of variation, and $k_1 = \dfrac{\text{area } abgd}{2a}$, in other words, if k_1 be the height of the median ordinate BD of the generalised curve, then the whole number of individuals in the population will be $k_1 c_1 \sqrt{\pi}$.

Now, suppose any destruction, which acts unselectively with regard to the organ in question, to reduce the number of individuals whose deviation lies between $\pm\, a$, to *cdef*, and let the $\dfrac{\text{area } cdef}{2a} = k_2$, or the height of the median ordinate BD^1. Since this destruction is unselective, it will destroy an equal percentage of animals of every deviation, and will therefore not alter the modulus. The population will therefore be reduced to $k_2 c_1 \sqrt{\pi}$ in number. This unselective destruction cannot be directly measured.

The selective destruction is most simply conceived as follows:—

In fig. 4 let AD^1HE represent a curve of modulus c_1, and let $BD^1 = k_2$, so that the area of the whole curve $AD^1HE = k_2 c_1 \sqrt{\pi}$ represents the population left after unselective destruction has occurred. Then suppose the modulus to be reduced during growth to c_2, where c_2 is less than c_1, and let AD^1KE be a curve of modulus c_2. The minimum number of individuals which it is necessary to destroy, in order to affect this reduction in the modulus, is evidently represented by the

Fig. 4.



shaded area of the figure. The population after such destruction is $k_2 c_2 \sqrt{\pi}$ in number, and the shaded area represents a number of individuals equal to $k_2 \sqrt{\pi}(c_1 - c_2)$, so that the ratio of animals selectively destroyed to animals which survive all unselective destruction is $\frac{c_1 - c_2}{c_1}$, a quantity which can be experimentally determined.

From the data given in Table III, this ratio, for frontal breadths of Plymouth crabs, becomes $\frac{10{\cdot}79 - 9{\cdot}96}{10{\cdot}79}$ or about 0·077, so that the hypothesis of selective destruction involves a death-rate of about 77 per thousand between the age corresponding to 12·5 mm. in carapace-length and maturity, as a consequence of deviation in frontal breadths, and in the group of structures, whatever these may be, which are directly correlated with it.

This total death-rate does not affect individuals of all deviations alike; an inspection of the figure will show that the death-rate is a function of the deviation, and that function is quite simply determined. Consider any ordinate Eg of the curve ABEC, and let its abscissa, DG, be of magnitude x; then the length of Eg is $k_2 e^{-x^2/c_1^2}$ and the number of individuals of deviation between x and $x + dx$ is $k_2 e^{-x^2/c^2} . dx$. In the same way, the height of the ordinate Fg is

$$k_2 e^{-x^2/c_2^2},$$

and the number of individuals of abnormality within unit distance of x after selection is

$$k_2 e^{-x^2/c_2^2} . dx.$$

The ratio between the number of animals of abnormality x which survive the unselective destruction and those which are selectively destroyed is therefore

$$\frac{\text{E}g - \text{EF}}{\text{E}g} = \frac{e^{-x^2/c_1^2} - e^{-x^2/c_2^2}}{e^{-x^2/c_1^2}} = 1 - e^{x^2(c_2^2 - c_1^2)/c_1^2 c_2^2}.$$

So that if g is the selective death-rate among animals of abnormality x, then that death-rate increases as x increases according to the equation

$$g = 1 - e^{-hx^2},$$

where h is the numerical value of $c_1^2 - c_2^2/c_1^2 c_2^2$, c_1 and c_2 being the values of the modulus at the time of its maximum value and at maturity respectively.

For the frontal breadth of Plymouth crabs, the value of h is about 0·015; so that of the whole number of animals which attain the size 12·5 mm., having an abnormality x of their frontal breadth, the fraction destroyed as a consequence of this abnormality before reaching maturity is

$$1-e^{-0\cdot015x^2}.$$

It will, of course, be understood that little trust can be placed in the absolute numerical results which are here put forward; the point which seems worthy of confidence, and which if it be indeed a reality is of very great importance, is the form of the result. For by purely statistical methods, without making any assumption as to the functional importance of the frontal breadth, the time of life at which natural selection must be assumed to act, if it acts at all, has been determined, and the selective death-rate has been exhibited as a function of the abnormality, while a numerical estimate which is at least of the same order as the amount of the selective destruction has been obtained.

The method by which the result described has been arrived at is likely to be capable of application to a very considerable number of cases. Mathematically considered, the conditions which were at first assumed and then proved to obtain in the organ discussed are by no means general. It is necessary for the employment of this method that the variations should be distributed on each side of the mean with sensible symmetry, and that the position of minimum selective destruction should be sensibly coincident with the mean of the whole system. Such statistical information as is at present available leads to the belief that these conditions may be expected to hold for a large number of species, which are sensibly in equilibrium with their present surroundings, so that their mean character is sensibly the best, and the change of mean from generation to generation is at least very small. They cannot be expected to hold in cases of rapid change such as those induced artificially by selection under domestication, or naturally by rapid migration or other phenomena resulting in a rapid change of environment.

For the investigation of such rapid change, it would be necessary to treat the more general case, in which the chances of deviations of opposite sign are not sensibly symmetrical, and in which the mean is not necessarily the position of minimum destruction. The treatment of this case requires the help of a professional mathematician.

It will be well to mention here a curious indirect confirmation of the result just described, based on evidence derived from a quite different source.

An attempt has been made to show that physiological accidents of a kind leading to change in the length of a portion of the carapace affect a crab at a rate measured by the value of the quantity $1-e^{-kx^2}$. The symmetrical distribution of variations from the mean which has been shown, especially by Mr. Galton, to occur in dimensions of weight, length, muscular strength, and other characters of various organs in men, moths, sweet peas, and other things at various periods of life, made it seem probable that if selective destruction could be shown to occur in these cases, the expression for intensity of destruction, in terms of the deviation, would in all these cases be of the same form as that already arrived at. That is to say, the expression for the effect of physiological accidents of a number of different kinds, affecting a number of organisms in no way specially alike, is probably always of the same form. The question at once occurred, whether this expression might not be of general application, as a measure of the effect of physiological accidents upon the animal body.

The most convenient case in which to look for an answer to this question is the case of muscular tissue, in which the effect of accidents of stimulus can be readily measured. The recent paper of Cyboulski and Zanietowski (Pflüger's 'Archiv f. Physiologie,' Bd. 56, p. 45) gives an excellent series of data for determining the relation between energy of stimulus applied to a nerve, and effect upon the muscle, as measured by energy of external work performed in contraction. These observers give a large series of tables, in which the energy of stimulus, applied by discharging a condenser of known electrical capacity through a nerve, is given in one column, and in another is the work done by the muscle stimulated, measured by the height through which a known mass is lifted.

As is well known, the application of stimuli of less than a certain magnitude produces no muscular contraction; but if the maximum stimulus which can be applied without causing a contraction be reckoned as zero, the subsequent relation between stimulus and contraction does, in fact, agree very closely with that indicated by successive values of the quantity $1-e^{-hx^2}$.

In spite of the evident care and skill with which Cyboulski and Zanietowski have performed their experiments, their curves are slightly irregular. In order to minimise the effect of these slight irregularities, three of their results were treated in the following way:—In each system of observations the maximum subliminal stimulus was subtracted from the magnitude of the applied stimulus in each case; the three numbers representing the height of the muscle contraction for unit stimulus beyond this point in the three cases were added together; and so on throughout. The result is plotted in fig. 5, the height of the sum of three contractions being indicated by the ordinates of the points ⊙; the intensity of the corresponding stimulus, *minus* the subliminal stimulus, being measured along the abscissa.

The dotted curve is given by

$$y = 1-e^{-x^2/(8\cdot15)^2},$$

8·15 being the "modulus" of the system of ordinates, determined from their moments about the axis of g. The coincidence between the two, rough as it is, is surely more than accidental!

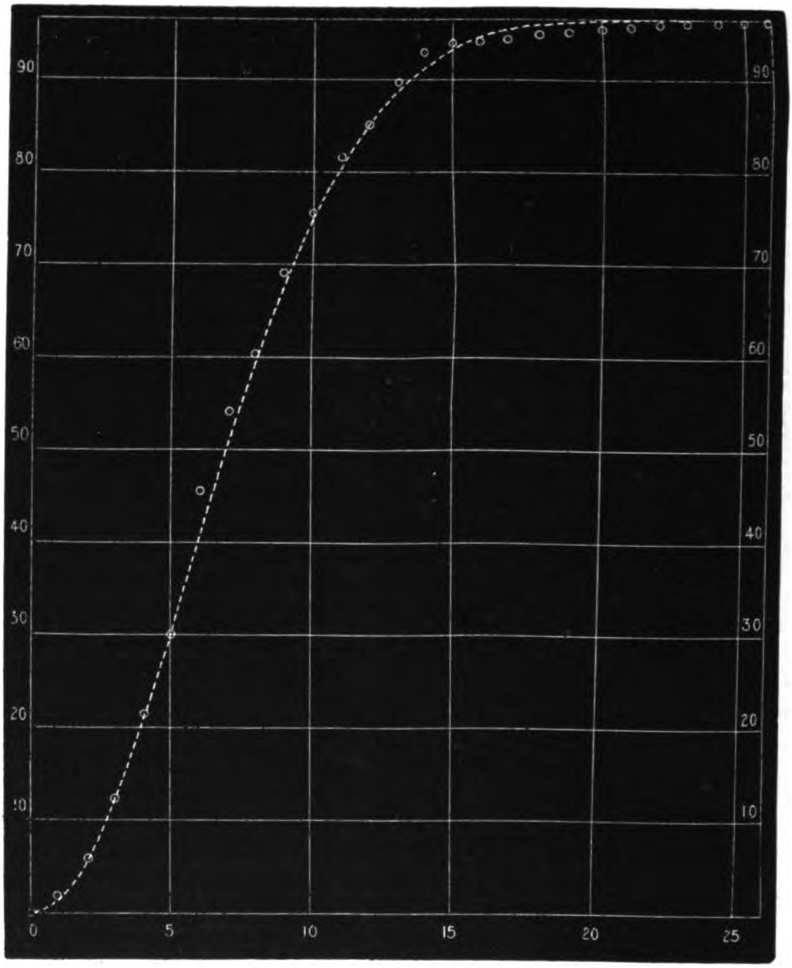


FIG. 5.—Sum of three Muscle-curves from Cyboulski and Zanietowski's paper. Each ordinate represents the sum of three muscle-contractions in millimetres: abscissæ represent stimulus applied to the nerve, expressed in ergs $\times 10^{-7}$, and reckoned from the close of the subliminal period.

The most interesting relation to be investigated in the light of this result would undoubtedly be the relation between sensation and stimulus in man; but existing data seem too imperfect to give any trustworthy result. It may be remarked that a few years ago measurements of the relation between muscle contraction and nerve stimulus, made with an imperfection comparable with that which characterises attempts to measure sensation, were held to obey a logarithmic law closely similar to the formula of Fechner and Weber.

II. *Variation in the Right Dentary Margin.*

The mean size of the right dentary margin was found to change, with increase of carapace-length, at such a rate as to render necessary the same subdivision of the material as that adopted in the case of frontal breadths. The change of mean will be gathered from Table IV, where it is seen that the change is slightly slower and less regular than in the frontal breadths, while its direction is reversed—the right dentary margin becoming larger, the frontal breadth smaller with increase of size.

Table IV.—Mean Length of Right Dentary Margin (D) expressed in thousandths of the Carapace-length (C) corresponding to various observed Carapace-lengths.

C.	D.	C.	D.
7·1	380·30	10·7	416·00
7·3	379·73	10·9	419·01
7·5	383·06	11·1	419·13
7·7	385·89	11·3	421·26
7·9	388·76	11·5	423·34
8·1	390·60	11·7	423·21
8·3	391·97	11·9	425·49
8·5	396·70	12·1	424·67
8·7	396·58	12 3	426·25
8·9	397·04	12·5	428·55
9·1	400·32	12·9	429·35
9·3	403·71	12·9	429·54
9·5	404·50	13·1	432·17
9·7	408·63	13·3	434·87
9·9	409·66	13·5	429·16
10·1	411·66	13·7	435·18
10·3	412·79	13·9	436·87
10·5	413·81	(Adult)	(495·14)

These observations were treated in the same way as those of frontal breadths; and the result of expressing the deviations from the mean in terms of the modulus of every group, and then summing deviations of corresponding magnitude, is shown in Table V, and graphically in fig. 6.

Table V.—Frequency of all observed Deviations from the Mean Length of the Right Dentary Margin in 8020 Female Crabs, Young and Adult, from Plymouth. Deviations in terms of the Modulus.

Limits of deviations.	Mean deviation.	Observed frequency.	Theoretical frequency.
	+5·530	1	
Over +3·20	+3·760	1	
	+3·340	1	
From +3·00 to 3·19	+3·120	1	2·76
„ +2·80 „ 2·99	+2·945	2	
„ +2·60 „ 2·79	+2·677	3	
„ +2·40 „ 2·59	+2·493	3	
„ +2·20 „ 2·39	+2·253	12	4·71
„ +2·00 „ 2·19	+2·050	9	11·29
„ +1·80 „ 1·99	+1·888	16	24·99
„ +1·60 „ 1·79	+1·705	45	51·14
„ +1·40 „ 1·59	+1·492	132	96·49
„ +1·20 „ 1·39	+1·276	155	168·30
„ +1·00 „ 1·19	+1·108	238	271·18
„ +0·80 „ 0·99	+0·897	375	403·41
„ +0·60 „ 0·79	+0·700	587	554·36
„ +0·40 „ 0·59	+0·493	735	703·61
„ +0·20 „ 0·39	+0·305	775	824·82
„ +0·00 „ 0·19	+0·112	939	893·04
„ −0·00 „ 0·19	−0·088	871	893·04
„ −0·20 „ 0·39	−0·270	833	824·82
„ −0·40 „ 0·59	−0·495	698	703·61
„ −0·60 „ 0·79	−0·739	553	554·36
„ −0·80 „ 0·99	−0·896	446	403·41
„ −1·00 „ 1·19	−1·093	240	271·13
„ −1·20 „ 1·39	−1·279	162	168·30
„ −1·40 „ 1·59	−1·479	89	96·49
„ −1·60 „ 1·79	−1·691	45	51·14
„ −1·80 „ 1·99	−1·932	18	24·99
„ −2·00 „ 2·19	−2·108	15	11·29
„ −2·20 „ 2·39	−2·295	6	4·71
„ −2·90 „ 2·59	−2·487	3	
„ −2·60 „ 2·79	−2·710	2	
„ −2·80 „ 2·99	−2·903	3	
	−3·330	2	
	−4·180	1	2·76
Over 3·00 ..	−4·830	1	
	−5·960	1	
	−7·030	1	

The symmetry of these results is fairly good, the number of positively abnormal individuals being 4030, the number of negatively abnormal 3990. The sum of the squares of the negative deviations is 2145·5; the sum of the squares of the positive deviations being 2099·9—a difference of about 2 per cent. This difference is greater than in the case of the frontal breadths; but a reference to the table will show that the removal of a single individual, namely, the indi-

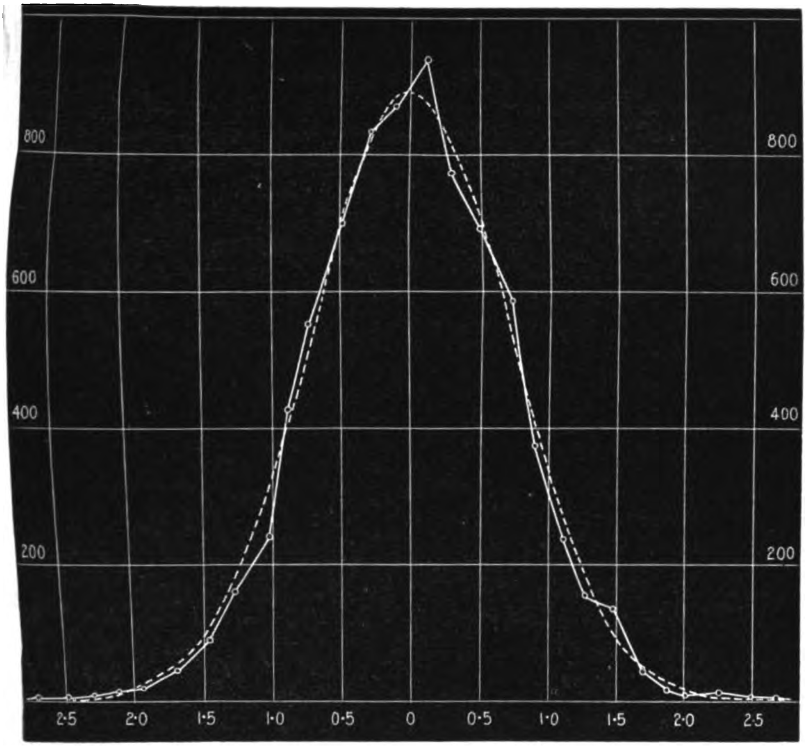


FIG. 6.—Deviations of 8020 measures of Right Dentary Margin in Female Crabs, old and young, from Plymouth Sound, expressed in terms of the Modulus. Eleven individuals of deviation greater than three times the Modulus are omitted.

vidual of deviation equal to −7 times the modulus, would make the sum of the positive and negative squares almost exactly equal.

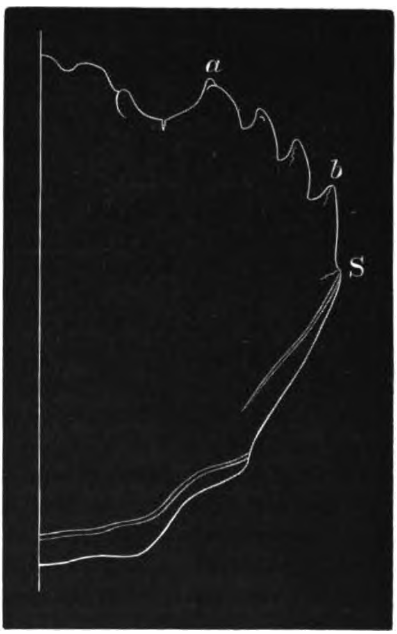
The mean error of the whole system is 0·5688 instead of 0·5642, or nearly 1 per cent. too great. The error of mean squares is 0·7276 instead of 0·7077, or 2·8 per cent. too great.

From these values of the mean error and error of mean square, as well as from the presence of a deviation so great as seven times the modulus, it is evident that some cause has been at work, producing large abnormalities with a frequency greater than that indicated by the theory of chance. Reference to the table shows that deviations of more that 2·5 times the modulus do in fact occur twenty times, instead of five or six times, as they should do So that deviations of this magnitude occur about three and a half times too often.

The sporadic occurrence of considerable deviations, which do not obey the general law of frequency of variation, is a phenomenon which has been supposed by many naturalists to be of great importance in evolution, and the present case is therefore worthy of discussion.

The following suggestion is offered as an explanation of the large *negative* deviations. As shown in Fig. 1, there are normally five teeth in the dentary margin; but occasionally (in over 1 per cent. of individuals) only four teeth occur. The reduction in teeth may apparently be effected in various ways: sometimes it is impossible to say that one tooth rather than another is missing; and the case then resembles those cases of variation in the segmentation of a vertebral column, for example, recently discussed by Bateson ("Materials for the Study of Variation," *passim*, especially, however, p. 124). In other cases, the reduction appears to be effected by a process resembling the filling up of the interval between two teeth, so that the points of the teeth project only very slightly. A careful outline of a specimen exhibiting this condition is given in fig. 7. It is evident that

FIG. 7.



in this case the little tubercle S which indicates the position of the fifth tooth is the point from which the measurement should be taken; but if the obliteration of the fifth tooth had progressed but a little further, no indication of its presence would remain; and the dentary margin, measured from the tip of the first to the tip of the last visible tooth, would really have been measured from *a* to *b*. Such a measure would not be homologous with the rest, and ought not to be included in the scheme. But, since reduction in the number of teeth may take place in other ways, and since it is impossible in a given case to distinguish the manner in which it has occurred, the measurements were necessarily recorded.

Another frequent cause of disturbance is the breakage of the last tooth, followed by its regeneration. All cases of obviously recent injury were of course excluded; and for this reason the total number of individuals discussed is reduced from 8069 to 8020. But the selection of material was felt to be so dangerous a proceeding that all cases in which there was any doubt as to the occurrence of an injury were included. The wrongful inclusion of a dozen such cases would account for the excess of positive abnormalities: for it is evident that a breakage of the tip of the last tooth would increase the distance AB in fig. 1.

While, therefore, the observations admit of the interpretation that about once in 500 cases a "sport" of magnitude greater than that provided for by the theory of chance does regularly occur, the considerations which have been submitted make this interpretation at least doubtful.

The value of the probable error, as an indication of percentage abnormality, is diminished by the existence of the large deviations discussed; but the values obtained are of considerable interest: they are as follows:—

Table VI.—Mean Value of Quartile Deviation (Q) of Right Dentary Margin for various Lengths of Carapace (C).

C.	Mean Q.
7·5	8·44
8·5	8·08
9·5	9·36
10·5	8·23
11·5	8·16
12·5	8·05
13·5	8·68
(Adult)	(9·28)

It will be seen from this table that the error of distribution at the ages measured is always less than in adult life, except among crabs, whose carapace length is between 9 and 10 mm. Of the fourteen superfluous deviations of great magnitude, three occur in this group, and the result is a quite untrustworthy determination.

Evidently, therefore, in spite of the abnormally great frequency with which large deviations occur, the whole percentage of abnormalities, among crabs between 7 and 14 mm. in length, is less than it is in adult crabs; and there is a rough agreement between the result obtained from these measurements and that obtained by Bowditch from the measurements of human stature already referred to. So that among female crabs in Plymouth Sound, during the period of life to which these observations refer, there is no indication of any destructive agency which acts selectively upon the dentary margin. Whether such selective destruction occurs among males, or among females at a later period of life, is for the present an open question.

Variation in frontal breadth may, therefore, for the present be considered to be of more importance in the economy of female crabs than variation in the length of the dentary margin—a view which receives confirmation from the dimorphism already shown to exist ('Roy. Soc. Proc.,' vol. 54, p. 324) in the frontal breadth of crabs from Naples, while it is a striking justification of the accepted system of classification, in which the characters of the great groups into which the Brachyura are divided are almost entirely those associated with changes in this dimension.

In conclusion, an important feature of the method employed may be pointed out. The increase of death-rate, associated with a given abnormality of frontal breadth, has here been roughly determined; in the previous paper, already referred to, the effect of abnormality in this dimension upon several other organs of the body was determined; and by the method of that paper it would be possible to determine the effect of parental abnormality upon the offspring. These are all the data which are necessary, in order to determine the direction and rate of evolution; and they may be obtained without introducing any theory of the physiological function of the organs investigated. The advantage of eliminating from the problem of evolution ideas which must often, from the nature of the case, rest chiefly upon guess-work, need hardly be insisted upon.

HARRISON AND SONS, Printers in Ordinary to Her Majesty, St. Martin's Lane.

[*From the* PROCEEDINGS OF THE ROYAL SOCIETY, Vol. 57.]

7

"Remarks on Variation in Animals and Plants. To accompany the first Report of the Committee for conducting Statistical Inquiries into the Measurable Characteristics of Plants and Animals." By Professor W. F. R. WELDON, F.R.S. Received February 19, 1895.

1. The importance of variation as a factor in organic evolution is not seriously disputed; but, if one may judge from the expressions contained in recent essays, naturalists are not agreed as to the

manner in which variation among individuals is associated with specific modification.

The view originally put forward by Darwin and Wallace is that specific modification is at least generally a gradual process, resulting from "the accumulation of innumerable slight variations, each good for the original possessor" ('Origin of Species,' chap. xv). This view rests on the assumption that each of those small differences which are to be observed among a group of individuals belonging to the same species has generally some effect upon the chance of life. "Can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind?" ('Origin of Species,' chap. iv).

Of late years, another view has received support from various writers. An examination of any series of animals of the same species preserved in a museum shows in most cases a large majority of specimens which are superficially alike: those individual differences, upon which stress is laid by Darwin and by Wallace, are often so slight as to escape attention unless minute comparison is made between individual and individual. But there will commonly be found a few individuals which differ so remarkably from their fellows as to catch the eye at once. Such large deviations differ from the smaller ones, at least in most cases, by their extreme rarity; but they have been extensively collected, and most museums contain numerous examples of their occurrence. Some naturalists have been led, from the striking character of such variations, to assume for them a preponderant share in the modification of specific character. These persons assume, if I understand them rightly, that the advantages or disadvantages which accompany the more frequent slight abnormalities are in themselves of necessity slight; and that the effect of such slight abnormalities may be neglected, in comparison with the effect produced by the occasional appearance of considerable deviations from the normal type. They regard change in specific character as an event which occurs, not slowly and continuously, but occasionally and by steps of considerable magnitude, as a consequence of the capricious appearance of "sports."

Without presuming to deny the possible effect of occasional "sports" in exceptional cases, it is the object of the present remarks to discuss the effect of small variations, as it may be deduced from the study of two organs in a single species.

The case chosen is the variation, during growth and in adult life, of two dimensions of female *Carcinus mœnas*, recently investigated by a Committee of the Royal Society; and what is here said may be considered an appendix to the report of that Committee.

2. The questions raised by the Darwinian hypothesis are purely statistical, and the statistical method is the only one at present obvious by which that hypothesis can be experimentally checked.

In order to estimate the effect of small variations upon the chance of survival, in a given species, it is necessary to measure *first*, the percentage of young animals exhibiting this variation; *secondly*, the percentage of adults in which it is present. If the percentage of adults exhibiting the variation is less than the percentage of young, then a certain percentage of young animals has either lost the character during growth or has been destroyed. The law of growth having been ascertained, the rate of destruction may be measured; and in this way an estimate of the advantage or disadvantage of a variation may be obtained. In order to estimate the effect of deviations of one organ upon the rest of the body, it is necessary to measure the average character of the rest of the body in individuals with varying magnitude of the given organ; and by the application of Mr. Galton's method of measuring correlation, a simple estimate of this effect may be obtained. In the same way a numerical measure of the effect of parental abnormality upon abnormality of offspring may be obtained by the use of Galton's correlation function, and such measurements have been made, in the case of human stature, by Mr. Galton himself.

It is to be observed that numerical data, of the kind here indicated, contain all the information necessary for a knowledge of the direction and rate of evolution. Knowing that a given deviation from the mean character is associated with a greater or less percentage death-rate in the animals possessing it, the importance of such a deviation can be estimated without the necessity of inquiring how that increase or decrease in the death-rate is brought about, so that all ideas of "functional adaptation" become unnecessary. In the same way, a theory of the mechanism of heredity is not necessary in order to measure the abnormality of offspring associated with a given parental abnormality. The importance of such numerical statements, by which the current theories of adaptation, &c., may be tested, is strongly urged.

3. The report itself describes an attempt to furnish some of the numerical data referred to for two dimensions of the shore crab. The data collected give an approximation to the law of frequency with which deviations from the average character occur at various ages. The conclusions drawn are (*a*) that there is a period of growth during which the frequency of deviations increases, illustrating Darwin's statement that variations frequently appear late in life; (*b*) that in one case the preliminary increase is followed by a decrease in the frequency of deviations of given magnitude, in the other case it is not; and that (*c*), assuming a particular law of growth (which

remains, as is admitted, to be experimentally tested), the observed phenomena imply a selective destruction in the one case, and not in the other.

It is not contended that the law of frequency at various ages, adopted in the report, is exact. It is, however, hoped that the approximation is sufficiently exact to give numerical estimates of the quantities measured, which are at least of the same order as the quantities themselves, and for this reason it is hoped that the method adopted may prove useful in other cases.

Harrison and Sons, Printers in Ordinary to Her Majesty, St. Martin's Lane.

Reprinted from the 'Veterinarian,' November, 1896.]

TELEGONY EXPERIMENTS:—THE BIRTH OF A HYBRID BETWEEN A MALE BURCHELL'S ZEBRA (*EQUUS BURCHELLI*) AND A MARE (*E. CABALLUS*).

By J. C. Ewart, M.D., F.R.S., Regius Professor of Natural History, University of Edinburgh.

In the second of the two short papers on Telegony* which I communicated last year to the *Veterinarian* I suggested a number of experiments which might be made with a view to settling, if possible, whether a previous sire has any influence on subsequent progeny obtained by other sires. At the same time I mentioned that I was making arrangements to carry out three of the experiments suggested, viz. (1) To cross a number of mares with a male Burchell's zebra, and then serve them with an Arab or other suitable horse. (2) To cross a zebra mare with an Arab horse, and then serve her with a zebra. (3) To cross an ass (*E. asinus*) with a zebra horse, and then serve her with a jackass.

Having begun in 1894 to make arrangements for the telegony and other investigations, I was in a position last summer to begin operations,†—that is to say, I had secured a large area of grass land and a small paddock; had provided accommodation for and purchased three Burchell's zebras (a horse and two mares), an Arab horse, a thoroughbred filly by "Petrarch," a mare by "Gunboat," and a number of ponies, including representatives from Ireland, Iceland, Shetland, and Norway. Further, Mr. Wilfrid S. Blunt, on hearing of the proposed experiments through the late Professor Goodhart, was generous enough to send me an Arab mare ("Bernabit"); and Lord Arthur Cecil,

* *The Veterinarian*, April and May, 1895.

† At Penicuik, Midlothian.

whom I had the good fortune to interest in my work, lent me "Mulatto," one of his Island of Rum ponies, and later added to my stud a young New Forest donkey.

It is hardly necessary to point out that even should the experiments in hand settle, or at least throw new light on the question of telegony, no final results are possible until, at the earliest, the summer of 1897. However, as the investigations are not limited to testing the influence of a previous sire, but either directly or indirectly deal with the development and ancestral history of the horse, with reversion or atavism, and polydactylism, and with various other problems of a more or less interesting nature, it may be well to put on record now some of the events that have happened since the work was started.

The Birth of the Zebra Hybrid.—The most interesting event I have to chronicle is the arrival of a hybrid between the Burchell zebra (Matoppo) and the West Highland pony (Mulatto). The hybrid, which, as announced in the *Field*,* was born on the 12th of August, is believed to be the first cross obtained between an ordinary mare and a zebra stallion. Partly on this account, and partly because zebra hybrids may help to solve the transport difficulties in South Africa, and do something towards overcoming the aversion for mules that has so long prevailed in England, a short account of the new arrival may not be unacceptable. But before speaking of the hybrid colt I ought to say a few words as to his parents. There are still three zebras found wild in Africa—two mountain zebras (*E. zebra* and *E. Grevyi*), and the zebra of the plains (*E. Burchelli*). The sire of the hybrid, as already indicated, is a Burchell's zebra which I obtained from the Antwerp Zoological Gardens.

Mr. G. R. de Courcy-Perry, H.B.M.'s Consul-General at Antwerp, to whom I am indebted for timely help at a critical moment, reported that the directors of the gardens considered their zebra stallion a superb animal; he is certainly the most handsome specimen I have ever seen. While in Antwerp "Matoppo" proved a successful sire, but it was only found possible to mate him with zebras of his own species. However, as a zebra long expected from South Africa never arrived, and as the Antwerp one was the only available mature male Burchell's zebra in Europe at the time, I had either to secure him or give up the experiments for another year.

Matoppo, last summer, was certainly very fastidious;

* *The Field*, August 22nd, 1896.

instead of a large crop of foals I am only able to report the arrival of one; but as a cross between a male zebra and a mare has apparently not been hitherto obtained, I ought perhaps to be thankful that the telegony experiments did not prove a complete failure. By carefully studying the habits of the zebra mares and Matoppo all the difficulties have been practically overcome; he no longer reminds one of the proverb, "You may lead a horse to the water, but you cannot make him drink." I need only add that the zebra horse, though low at the withers, stands thirteen hands (52 inches) high; that he is beautifully marked, and in his form and movements suggests a horse far more than either of the mountain zebras; further, his action when trotting is even more perfect than that of his stable companion the high-caste Arab horse, Benazrek.

Mulatto, the dam of Romulus, is a West Highland pony, and is 13.1 (53 inches) high. Lord Arthur Cecil, who has taken a lively interest in the investigations from the outset, first intended sending a couple of New Forest ponies. After further consideration he, for various reasons, selected Mulatto; this has proved a most fortunate selection. Apart from the all-important fact that Mulatto has produced a foal to the zebra, she is in many ways pre-eminently suitable for the experiments in hand. From information kindly supplied by his lordship, it appears that the breed to which her sire belongs has been for many years all but completely isolated on the Island of Rum, a small island lying between the mainland of Scotland and the Outer Hebrides. As far as is known, fresh blood has only once been introduced during recent times into the Island of Rum; this was in 1848, when the then proprietor of the island, the late Marquis of Salisbury, sent to Rum a thoroughbred stallion. Mulatto's dam came from the Long Island (Outer Hebrides), but she belonged to the same breed as the sire. Like Mulatto and all her ancestors, as far as they can be traced, the dam was jet-black, and, like almost all this particular breed of ponies, her eyes were of a hazel colour—not brown, as in the majority of horses. In Mulatto there is only a faint indication of the characteristic hazel-coloured iris. It is difficult to account for the existence of more or less isolated herds of well-bred ponies in the Western Highlands. The late Marquis of Salisbury believed that, notwithstanding their colour, they had Eastern blood in their veins. It has been suggested that they numbered amongst their ancestors horses which escaped from the ill-fated ships of the Spanish Armada. In support of this belief it may be mentioned that an old tapestry in the House of Lords (a representation of which appeared some years ago in the *Illustrated London News*) indicates that storms overtook the Spanish fleet at several points off the Western Islands; it may be more than a coincidence that well-bred ponies were afterwards found on islands adjacent to the storm areas—on islands and parts of islands to which the dismantled Armada ships might very well have drifted. Further, the Mulatto breed of ponies resembles well-bred black horses often met with in Spain at the present day. Whatever the origin of the ponies in question, it is enough that they belong to a distinct breed, and that probably only once (in 1848) during many generations has fresh blood been introduced into the isolated and somewhat inaccessible Island of Rum, from whence Mulatto's sire was exported in 1888. As a proof of the isolation, or, in other words, of in-breeding, crosses between Island of Rum ponies and other breeds present nearly all the characters of the West Highland race.

Mules generally strongly resemble their asinine progenitors, but the mules bred by the late Marquis of Salisbury in the Island of Rum were observed on reaching Hatfield to resemble ponies rather than donkeys; this, to my mind, proves that Mulatto belongs to a well-marked and distinct breed, and that whatever the result may eventually be, she is in every way as suitable, as well adapted for taking the place of the nearly purely bred Arab mare used in Lord Morton's famous experiment, as the zebra Matoppo is an excellent substitute for the now extinct or all but extinct quagga. It is only necessary to add, before proceeding to describe the hybrid, that the foals of the black Highland ponies are frequently at first mouse-coloured, with in some instances a faint dorsal stripe, and a patch of dark hair at the shoulders, which represents the bands so often seen in dun-coloured Norwegian ponies. The dorsal stripe usually disappears soon after birth, and the mouse-colour never reappears when the first or foal's coat is once shed.

Turning now to the hybrid, I may first mention that the period of gestation was normal, 342 days. With the mare it varies from 340 to 350 days. In the zebra it is said to extend over, as in the ass, twelve months. Within a minute after birth the hybrid was rushing about as if he were a young zebra, whose existence depended on his at once joining the troop of which his dam was a member.

Being extremely alert, and ready to gallop off at any moment, he seemed at a loss to understand the inaction of his placid dam. Though he is now, when two months old, no longer so restless, or like a timid young animal whose only safety is in flight, Romulus is still surprisingly energetic, and he seems to enjoy nothing better than coursing about his paddock as if he were escaping from some dreaded foe. He is now wonderfully tame, and courts rather than shuns notice; and from the first he has behaved himself quite differently from a young New Forest mule I had the opportunity of constantly watching during last summer. In nearly all his movements Romulus resembles his sire rather than his dam; he has not the dainty action of a young mule or a young donkey, and yet he differs in his gait from a horse. As he grows older I anticipate the beautiful action of the zebra will become more and more apparent. The Arab mare, Bernabit, when set free in the park, tosses her head high in the air in a most suggestive way as she gallops about. The zebra horse, on the other hand, carries his head low, and twists his neck as if engaged in single combat, ready to seize the limbs of an adversary. In his gambols the hybrid carries himself like a zebra, and this without once having had an opportunity of seeing Matoppo disporting himself.

When in the field with mares the zebra horse herds them most jealously; should anyone appear on the scene he gallops along uttering his war cry, prepared to defend his herd against all comers. I shall not be surprised should Romulus imitate his father in this also, should an opportunity offer by-and-by.

As the time drew near for the birth of the hybrid I became more and more curious as to which of its parents it would most resemble in shape and colour. When two distinct types are crossed the progeny may present the characters of both parents, or may closely resemble one of the parents, or by reverting to the ancestral type differ decidedly from all the immediate progenitors. For example, mules sometimes closely resemble donkeys, at other times they resemble ponies. Again, if a white fantail is crossed with a white pouter, the young may resemble a blue rock, the remote ancestor of all the pigeons. There has probably been no intercrossing for many thousands of years between zebras and the other wild Equidæ, and it is quite possible there has not even been interbreeding between the Burchell and the other zebras. On the other hand, there is always a chance that any given zebra has been inbred. Horses, on the other hand, with a few possible exceptions, have been interbreeding in all parts of the world; and though sometimes inbred, they at the best are far less fixed and stable than the zebras. Consequently, on *a priori* grounds, I expected the hybrid to resemble at least in colour a zebra rather than a horse. I had no very decided opinion as to the shape of the hybrid, but I did not believe what some would-be prophets asserted, that the only result of my experiments would be the production of a monster; that it was little short of sacrilege to cross a good mare with a zebra. Whatever form or colour the hybrid may ultimately assume, I have no hesitation in saying that it would be difficult to imagine any more attractive, more graceful, or more beautiful member of the equine family than the little hybrid zebra has been during the first two months of his existence.

Never ungainly, Romulus is now as complete and compact as a little horse, and he looks at least twice his age, notwithstanding his being a late foal, and the untoward weather that has prevailed since he appeared on the scene. This is probably partly due to his beginning to feed on his own account at a very early period. When three days old he was nibbling grass; a few days later he attacked hay, and now he insists on having a share of the oats provided for his dam. Foals frequently content themselves with milk alone during the early weeks.

In shape the hybrid unites the characters of both his parents, and yet without approaching a mule differs from both. When standing on the alert at a little distance, he looks as if he had slipped down from a frieze on the Parthenon. The muzzle is very fine, with narrow, almost slit-like nostrils of the distinctly zebra pattern. The forehead is wide as in an Arab, and very slightly convex from side to side. The jaws look narrow, and the head seems to be set on the neck in an uncommon fashion, and the neck is somewhat short. In the neck and its relation to the head,
m ~~so~~ the position and length of the ears, and in the mane, the hybrid undoubtedly approaches more closely to a zebra than a horse. But beyond the root of the neck I fail to observe any essential difference from a half-bred Arab foal occupying an adjacent box. Both the fore and hind quarters are well formed; the back is short and strong, and the chest is wide and well moulded. In the form of the fore and hind limbs, and in the hoofs, Romulus also resembles the half-bred Arab; and his tail, with the exception of several bands at the root and the presence of somewhat

Mulatto, and Romulus when five days old. From a photograph by Swan Watson, Edinburgh.

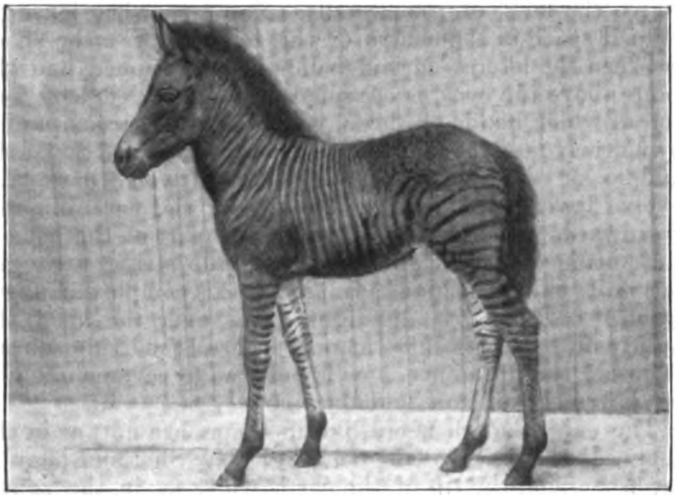
stiff hairs, agrees with that of an ordinary foal. As in the zebra, there are rudimentary teats, the chestnuts are absent in the hind limbs, and further there is no tuft of hair at the fetlocks. A little bit in front of the upright mane there is a separate tuft of hair as in the zebra, and as in many, if not all foals. In the foal this tuft of hair is mainly concerned in forming the forelock.

The Colour and Striping of the Hybrid.—Darwin, who devoted much time to studying the colour of the horse, came to the conclusion that all the existing races had descended from "a single dun-coloured, more or less striped, primitive stock, to which our horses occasionally revert." In Dzungaria there appear to be still wild horses, *i.e.* horses whose ancestors have never been domesticated. The wild horses of North America, which were believed to have descended from the Spanish horses of Mexico, were of all colours—black, grey, roan, sorrel, &c.; but the Dzungaria horses are all of one colour. In summer they are dun or sandy coloured; in winter light brown. In all probability the Dzungaria wild horses have not departed greatly from the ancestral shade. The absence of shoulder and leg bands on these wild horses is interesting. We shall never get beyond guessing when the stripes first appeared in the horse group, but it may be assumed that it was long after the dun colour was finally adopted.

Compared with the even-toed ruminants (oxen, sheep, deer, antelopes, &c.), the odd-toed ungulates have suffered heavily during the Tertiary period,—only the tapir, the rhinoceros, and the horse families have survived. This being the case, it may be taken for granted that at least in some areas the struggle for existence in the case of the non-ruminating ungulates was very keen. Bearing this in mind, the existence of stripes becomes intelligible if it be admitted that they counted for something in the battle of life. Before, however, admitting that the ancestor of all the horses was "more or less striped," it is well to remember that the only wild horse we are acquainted with (*E. Przewalskii*) has but a faint dorsal band; and that while stripes were presumably useful in races living in wide, fertile, richly populated plains, they may not have been necessary in the case of the Dzungaria and other races living in remote desert regions.

In considering the colour of the hybrid it is also well to remember that when distinct types are crossed the progeny are apt to revert to a more primitive type, to assume some of the ancestral colours.

Taking these and other facts into consideration, I expected the hybrid at birth to be of a dun or bay colour, with distinct dark stripes on the legs and shoulders, and less distinct stripes on the face. I was not a little surprised when I found Mulatto's foal extremely well provided with stripes all over, in some respects more richly, if less obtrusively, decorated than any of the zebras. As might



Romulus, twenty-seven days old. From a photograph by Reid, Wishaw.

have been anticipated, the majority of the stripes were intensely black, while the groundwork varied from a light tan colour on the lower part of the legs to a rich brown on the lower part of the face. On the under aspect of the neck and trunk, however, the dark stripes were indistinct; this was especially true of the ventral mesial band which blended with the dark body colour at each side. When the markings of the hybrid are carefully contrasted with the stripes in the three living zebras, they will be found to differ very considerably, more especially in the head region and over the loins and hind quarters. In the meantime I shall content myself with shortly describing the disposition of the stripes in the hybrid. The head is characterised by having a remarkable series of dark brown narrow bands, which alternate with a corresponding series of equally narrow bright tan-coloured bands. Beginning on a level with the eyes these bands extend upwards, forming a number of graceful arches which at once remind one of the forehead of an elaborately tattooed Maori chief. Fourteen pairs of these bands can easily be made out, but the upper ones are interrupted by the tuft of hair representing a forelock. Curving downwards from within the eyes towards the nostrils are other bands of a similar width and colour, which serve to decorate the sides of the face. These stripes eventually lose themselves in the rich brown hair above the level of the nostrils. The somewhat lozenge-shaped space in the centre of the forehead, *i.e.* the space between the lateral curved bands just mentioned and the loops above the eyes, is occupied by a U-shaped loop, one end of which bends upwards, while the other, accompanied by a nearly mesial stripe, runs for some distance down the middle of the face. Similar bands (twelve dark and twelve light) extend from the base of the ear obliquely downwards over the jaw. The greater part of the head is thus tattooed with bright-coloured narrow stripes arranged in a quite unique fashion. In having this complex arrangement of narrow dark and light bands over the head, the hybrid differs in a striking manner from all the living zebras. Whether the difference is or is not due to reversion it will be extremely difficult to determine.

The ears, though zebra-like in shape, are not, as in the zebra, distinctly banded. In a light bay Shetland pony in my possession the tip of the ear is white as in the zebra, but in Romulus the upper third of the ear is of a dark brown colour. This colour extends as a broad band towards the base, where it is interrupted by tan-coloured patches having in the main a transverse course. The entire ear is lined with a thick coating of fine long bright yellow hair. In a front view the light-coloured ears, with the dark upright mane between them, are almost as conspicuous as the corresponding structures in the zebra.

As is usually the case in the zebras, a dark band extends downwards from the withers, to bifurcate at the shoulder, the one limb running forwards to the chest, the other backwards behind the elbow. In front of this, which may be known as the shoulder stripe, are a number of cervical stripes, some of which blend as they run across the neck. At the root of the mane, in front of the shoulder stripe, twenty dark bands alternate with a corresponding number of light ones. The latter are continued some distance into the mane by light brown hairs. The last of the cervical bands meet, as in the zebra, in the middle line over the sternum, and become continuous with a broad but not very well-defined ventral band, consisting of long dark brown hairs. Running downwards across the trunk, behind and nearly parallel with the shoulder stripe from the withers, are nine bands, which take the place of the four or five broad vertical bands in Burchell's zebra. Behind these are four bands which curve upwards and backwards, but instead of extending obliquely across the hind quarters, as in the sire, they lose themselves amongst the dots and short transverse stripes which occupy the region of the loins and the upper part of the hind quarters. In having these dark dots and short narrow stripes over a part of the back the hybrid differs from all the zebras.

It will be interesting to note if there is a like failure to develop distinct broad bands over the hind quarters in hybrids that may afterwards be obtained. The remarkable colouring of the back is more likely to be due to reversion than the elaborate decoration of the face, and it may have some relation to the dappling so common over the quarters in most breeds of horses. There is a distinct dark dorsal stripe, with a yellow band at each side, extending along the middle line to the root of the tail. The dorsal stripe, narrow in front, expands considerably as it proceeds backwards. The tail, as in the zebra, has several cross-bands at its root. In the region of the shoulder-joint there is again a failure to form distinct stripes, but there are numerous bands across both the fore and hind limbs. Twenty-four bands were counted on the left fore-limb, and thirty-one on the left hind limb. The twelve below the knee run obliquely downwards and backwards, and become fainter as the fetlock is reached, while those on the knee and the forearm are well marked, and almost form complete circles. In the hind limb the bands above and for a short distance below the hock are extremely well marked, while those on the shank and over the fetlock and pasterns are only represented by faint, short, oblique stripes, which fail to reach the inner surface. As in the zebra, there are narrow incomplete stripes dividing the broad spaces between the well-marked dark bands of the thigh and upper part of the leg.

Without giving further details it will be evident, with the help of the figures, that the hybrid is elaborately striped, and that it profoundly differs from an ordinary foal. If the figures are compared with photographs of any of the zebras, and more especially with a photograph of a Burchell's zebra, numerous differences in the disposition and in the number of the stripes will be readily noticed.

Should the next foal, as was said to be the case in the purely bred second and third foals of Lord Morton's mare, be still more banded, or even provided with a fraction of the bands seen in the photograph, a very good case will have been made out for telegony.

It is still impossible to say what colours the hybrid will eventually assume, but I believe a number of the bands will all but disappear, and that the dark stripes will be separated from each other by brown or dun-coloured bands or spaces. It is quite possible the hybrids bred from light-coloured mares may retain a light body colour and, even when full-grown, have the stripes as distinct as a zebra.

Before leaving the hybrid I may point out that its existence raises a number of interesting questions. In 1808, Frederic Cuvier published in the *Annals du Muséum d'Histoire Naturelle* * a note on the mating of an Arab horse with a zebra mare which had previously bred to a male donkey. Unfortunately the mare died some months before the period of gestation was completed. Since then several hybrids have been bred between zebra mares and ponies, but apparently a hybrid between a pony mare and a zebra horse has not hitherto been obtained. Mules, *i. e.* hybrids between a jackass and mares, are alike common and valuable; while hinnies, *i. e.* hybrids between a pony and a she-ass, are rare in England and comparatively unimportant. In the same way, while hybrids between ponies and zebra mares are not likely ever to be of much use, hybrids between a zebra stallion and ordinary mares (what some would call zebra mules) may have a great future before them. Captain Lugard, who has done splendid but insufficiently acknowledged pioneer work, more especially in East Africa, recommended some years ago "that an attempt should be made to obtain zebra mules by horse or donkey mares," because he believed such mules "would be found excessively hardy, and impervious to the fly [the dreaded tsetse fly], and to climatic diseases."

Captain Lugard believed "that their export might prove one of the sources of wealth and revenue in the future;" for, as he adds, "every one knows the paucity of mules, both for mountain batteries and for transport purposes, has long been one of the gravest difficulties in our otherwise almost perfect Indian Army corps."† Like Mr. Tegetmeier,‡ I have been assured that zebra mules would be

* Vol. ii, p. 237. † 'Our African Empire.'
‡ *Live Stock Journal*, 25th Sept., 1896.

great favourites with the natives in India, and further, it is supposed they might prove invaluable in the West Indies. I have already mated seven different breeds of mares with the zebra, mares varying in size from 11 to 15 hands, and, in fact, enough has been already accomplished to show that zebra hybrids could be produced suitable, as far as make and size go, for all kinds of work. Further, I had last summer a Burchell's zebra filly that was perfectly docile, in every way as domesticated as a Shetland pony. Hence from a mental as well as from a physical standpoint I fail to see why zebra hybrids should not, if properly handled, prove as serviceable to man as either mules or horses—in some cases even more so.

Another question of interest is, will the zebra mules breed *inter se*, or with horses, zebras, or asses, or any of their hybrids? This is a question which it is impossible to answer until experiments have been made. Because ordinary mules have never been known to breed it is argued zebra mules must be infertile. But this does not necessarily follow, for as zebras differ from donkeys, so may zebra hybrids (even in the matter of fertility) differ from mules. Darwin writes, "Many years ago I saw in the Zoological Gardens a curious triple hybrid, from a bay mare by a hybrid from a male ass and a female zebra."* This is a case of an equine hybrid (*i. e.* a male hybrid obtained by crossing a zebra mare with a jackass) being fertile when mated with a pony mare. Granting the information given Mr. Darwin was correct, this case proves that even in the horse family hybrids may be fertile, and strongly indicates that very careful attempts should be made to get the new zebra hybrids to breed.

Turning from the zebra hybrid, the next most important fact to chronicle is that, by taking advantage of the knowledge gained as to the habits of zebras, there is now in some respects less difficulty and danger in using Matoppo for stud purposes than there is in using many ordinary stallions. And further, Matoppo has been trained without applying any severe measures whatever, and without making him less a wild animal than he was on his arrival. By gentle treatment he has become quite tractable. Some days ago I observed the stud groom pulling Matoppo's tail with the object of bringing him round to drink. This is one side of the shield; but there is another, for the same groom would be at once attacked, should he interfere with Matoppo when mares are in his vicinity.

* 'Animals and Plants under Domestication,' vol. ii, p. 16.

Under such circumstances Matoppo is quite regardless of whips or any other instruments of a like nature.

In concluding my remarks on the zebras I may mention that, like Frederic Cuvier in 1807, I had no difficulty in mating the five-year-old zebra mare with the Arab horse Benazrek; but unfortunately this mare succumbed during the winter. The two-year-old zebra filly which I found so docile and attractive also died; and having failed to secure a grant in aid of my investigations from the money set apart by Government for the promotion of research or from any other source, I have not yet been in a position to replace the zebra mares.

In addition to working with zebras I attempted various crosses with donkeys and with an Indian (zebu) bull, but so far I have failed to obtain any results.

In connection with my investigations bearing on polydactylism and on the development of the horse I may mention that I have now in my possession several specimens showing extra digits in the horse and a considerable number of horse embryos. Amongst others I have an embryo for each of the weeks from the fourth to the eighth inclusive, but I have been again and again disappointed in my efforts to secure a three-weeks' embryo.* I have already shown† that in a horse embryo fourteen inches in length the second and fourth digits, though extremely small, are present. I am now in a position to state that at the fifth week the second and fourth digits are nearly as long and as well developed as the third or middle digit, —that, in other words, the horse is for a time tridactylous, the outer digits being relatively as large as in the adult rhinoceros.

In addition to studying the embryos I have been examining the fœtal appendages. The most interesting facts made out in connection with these appendages are, first, that the rudiments of the fœtal villi make their appearance between the sixth and seventh weeks, and are well formed by the end of the eighth week; and second, that as the yolk placenta dwindles, a complex epiblastic girdle appears externally, while numerous apparently non-vascular villi grow out from the allantois into the cœlomic space between

* As a considerable number of young embryos will be required, I shall be very grateful for horse or donkey embryos under six inches in length. The embryos should, if possible, be placed for twenty-four hours in a saturated solution of corrosive sublimate, and then forwarded in 50 per cent. spirit. But if not absolutely fresh, they should be at once placed in 75 per cent. spirit.

† *Journal of Anatomy and Physiology*, April, 1894.

the rapidly growing allantois and the equally rapidly shrinking yolk-sac.

I have also made some observations as to the condition of the ovaries during gestation. To admit of further observations being made, I shall be greatly obliged if ovaries are sent me as opportunity offers, information being sent in each case as to the period of gestation reached in the subject from which they were taken.

Postscript.—I find I have omitted to mention that Romulus is Mulatto's first foal, and that his eyes are of a bluish-grey colour, somewhat darker than in his sire, Matoppo.

Appendix.—Measurements of Romulus (in inches) when two months old: withers to the ground, 38½; shoulder—joint to the ground, 29; elbow to the ground, 26½; elbow to the fetlock, 20½; cannon bone along outside, 8; diameter at knee, 8½; diameter below knee, 5; withers on a line with anterior border of scapula to root of tail, 27½; withers to occipital protuberance, 19; chest to buttocks, 35; girth behind fore-legs, 39; length of head from occipital protuberance to end of muzzle, 16½; width between eyes where narrowest, 5½; where widest, 9½; length of ear, 5¼; stifle to hock, 13; hock to the ground, 18; diameter of head above nostrils, 11¼; neck at junction with head, 19; diameter of fore-pasterns, 5; diameter of hind pasterns, 5½; diameter of shanks, 5½; diameter of fetlock-joints, 7¼; diameter of coronets, 7¾.

PRINTED BY ADLARD AND SON,
BARTHOLOMEW CLOSE, LONDON, E.C., AND 20, HANOVER SQUARE, W.

WEISMANNISM ONCE MORE

BY

HERBERT SPENCER

Reprinted from "The Contemporary Review" with a Postscript

WILLIAMS & NORGATE
14 HENRIETTA STREET, COVENT GARDEN, LONDON
1894

NOTE.

PROF. WEISMANN'S Romanes Lecture, delivered at Oxford, May 2, 1894, was a re-rejoinder, partly indirect and partly direct. In it he dealt with certain arguments I had brought forward in my "Rejoinder," &c. published in *The Contemporary Review* for December 1893; and it is to be presumed that he used in that lecture all his arguments of chief importance.

To it, when printed, he appended numerous notes; and he had the opportunity of publishing among them any such additional reasons for dissenting from my views as occurred to him. Hence he may fairly be supposed to have now completed his case.

In the succeeding essay I have proceeded upon this supposition: assuming that, about matters on which he has said nothing further, he has nothing further to say.

On the last page will be found a postscript containing facts of much significance, not included in the essay as published in *The Contemporary Review* for October 1894.

H. S.

64 AVENUE ROAD,
REGENT'S PARK, LONDON, N.W.
October 1894.

WEISMANNISM ONCE MORE.

AMONG those who follow a controversy to its close, not one in a hundred turns back to its beginning to see whether its chief theses have been dealt with. Very often the leading arguments of one disputant, seen by the other to be unanswerable, are quietly ignored, and attention is concentrated on subordinate arguments to which replies, actually or seemingly valid, can be made. The original issue is thus commonly lost sight of.

More than once I have pointed out that, as influencing men's views about Education, Ethics, Sociology, and Politics, the question whether acquired characters are inherited is the most important question before the scientific world. Hence I cannot allow the discussion with Professor Weismann to end in so futile a way as it will do if no summary of results is made. Here, therefore, I propose to recapitulate the whole case in brief. Primarily my purpose is to recall certain leading propositions which, having been passed by unnoticed, remain outstanding. I will turn, in the second place, to such propositions as have been dealt with; hoping to show that the replies given are invalid, and consequently that these propositions also remain outstanding.

But something beyond a summing-up is intended. A few pages at the close will be devoted to setting forth new evidence which has come to light since the controversy commenced—evidence which many will think sufficient in itself to warrant a positive conclusion.

The fact that the tip of the fore-finger has thirty times the power of discrimination possessed by the middle of the back, and that various intermediate degrees of discriminative power are possessed by various parts of the skin, was set down as a datum for my first argument. The causes which might be assigned for these remarkable contrasts were carefully examined under all their aspects. I showed in detail that the contrasts could not in any way be accounted for by natural selection. I further showed that no interpretation of them is afforded by the alleged process of panmixia: this has no *locus standi* in the case. Having proved, experimentally, that ability of the fingers to discriminate is increased by practice, and having pointed out that gradations of discriminativeness in different parts correspond with gradations in the activities of the parts as used for tactual exploration, I argued that these contrasts have arisen from the organized and inherited effects of tactual converse with surrounding things, varying in its degrees according to the positions of the parts—in other words, that they are due to the inheritance of acquired characters. As a crowning proof I instanced the case of the tongue-tip, which has twice the discriminativeness of the fore-finger-tip: pointing out that consciously, or semi-consciously, or unconsciously, the tongue-tip is perpetually exploring the inner surfaces of the teeth.

Singling out this last case, Professor Weismann made, or rather adopted from Dr. Romanes, what professed to be a reply but was nothing more than the blank form of a reply. It was said that though this extreme discriminativeness of the tongue-tip is of no use to mankind, it may have been of use to certain ancestral *primates*. No evidence of any such use was given; no imaginable use was assigned. It was simply suggested that there perhaps was a use.

In my rejoinder, after indicating the illusory nature of this proceeding (which is much like offering a cheque on a bank where no assets have been deposited to meet it), I pointed out that had the evidence furnished by the tongue-tip never been mentioned, the evidence otherwise furnished amply sufficed. I then drew attention to the fact that this evidence had been passed over, and tacitly inquired why.

No reply.*

In his essay on "The All-Sufficiency of Natural Selection," Professor Weismann set out, not by answering one of the arguments I had used, but by importing into the discussion an argument used by another writer, which it was easy to meet. It had been contended that the smallness and deformity of the little toe are consequent upon the effects of boot-pressure, inherited from generation to generation. To this Professor Weismann made the sufficient reply that the fusion of the phalanges and otherwise degraded structure of the little toe, exist among peoples who go barefoot.

In my "Rejoinder" I said that though the inheritance of acquired characters does not explain this degradation in the way alleged, it explains it in a way which Professor Weismann overlooks. The cause is one which has been operating ever since the earliest anthropoid creatures began to decrease their life in trees and increase their life on the earth's surface. The mechanics of walking and running, in so far as they concern the question at issue, were analyzed; and it was shown that effort is economized and efficiency increased in proportion as the stress is thrown more and more on the inner digits of the foot and less and less on the outer digits. So that thus the foot furnishes us simultaneously with an instance of increase from use and of decrease from disuse: a further disproof being yielded of the allegation that co-operative parts vary together, since we have here co-operative parts of which one grows while the other dwindles.

* In "The All-Sufficiency of Natural Selection" (*Contemporary Review*, Sept. 1893, p. 311), Professor Weismann writes:—"I have ever contended that the acceptance of a principle of explanation is justified, if it can be shown that without it certain facts are inexplicable." Unless, then, Prof. Weismann can show that the distribution of discriminativeness is otherwise explicable, he is bound to accept the explanation I have given, and admit the inheritance of acquired characters.

I ended by pointing out that, so far from strengthening his own case, Professor Weismann had, by bringing into the controversy this changed structure of the foot, given occasion for strengthening the opposite case.

No reply.

We come now to Professor Weismann's endeavour to disprove my second thesis—that it is impossible to explain by natural selection alone the co-adaptation of co-operative parts. It is thirty years since this was set forth in *The Principles of Biology*. In § 166 I instanced the enormous horns of the extinct Irish elk, and contended that in this, and in kindred cases, where for the efficient use of some one enlarged part many other parts have to be simultaneously enlarged, it is out of the question to suppose that they can have all spontaneously varied in the required proportions. In "The Factors of Organic Evolution," by way of enforcing this argument, which had, so far as I know, never been met, I dwelt upon the aberrant structure of the giraffe. And then, in the essay which initiated this controversy, I brought forward yet a third case—that of an animal which, previously accustomed only to walking, acquires the power of leaping.

In the first of his articles in the *Contemporary Review* (September 1893), Professor Weismann made no direct reply, but he made an indirect reply. He did not attempt to show how there could have taken place in the stag the "harmonious variation of the different parts that co-operate to produce one physiological result" (p. 311); but he contended that such harmonious variation *must* have taken place, because the like has taken place in "the neuters of state-forming insects"—"animal forms which do not reproduce themselves, but are always propagated anew by parents which are unlike them" (p. 313), and which therefore cannot have transmitted acquired characters. Singling out those soldier-neuters which exist among certain kinds of ants, he described (p. 318) the many co-ordinated parts required to make their fighting organs efficient. He then argued that the required simultaneous changes can "only have arisen by a selection of the parent-ants dependent on the fact that those parents which produced the best workers had always the best prospect of the persistence of their colony. No other explanation is conceivable; *and it is just because no other explanation is conceivable, that it is necessary for us to accept the principle of natural selection*" (pp. 318–9).

[This passage initiated a collateral controversy, which, as continually happens, has greatly obscured the primary controversy. It became a question whether these forms of neuter insects have arisen as Professor Weismann assumes, or whether they have arisen from arrested development consequent upon innutrition. To avoid entanglements I must for the present pass over this collateral controversy, intending to resume it presently, when the original issues have been dealt with.]

No one will suspect me of thinking that the inconceivability of the negation is not a valid criterion, since, in "The Universal Postulate," published in the *Westminster Review* in 1852 and afterwards in *The Principles of Psychology*, I contended that it is the ultimate test of truth. But then in every case there has to be determined the question—*Is* the negation inconceivable; and in assuming that it is so in the case named, lies the fallacy of the above-quoted passage. The three separate ways in which I dealt with this position of Professor Weismann are as follows:—

If we admit the assumption that the form of the soldier-ant has been developed since the establishment of the organized ant-community in which it exists, Professor Weismann's assertion that no other process than that which he alleges is conceivable, is true. But I pointed out that this assumption is inadmissible; and that no valid conclusion respecting the genesis of the soldier-ant can be drawn without postulating either the ascertained, or the probable, structure of those pre-social, or semi-social, ants from which the organized social ants have descended. I went on to contend that the pre-social type must have been a conquering type, and that therefore in all probability the soldier-ants represent most nearly the structures of those ancestral ants which existed when the society had perfect males and females and could transmit acquired characters, while the other members of the existing communities are degraded forms of the type.

No reply.

A further argument I used was that where there exist different castes among the neuter-ants, as those seen in the soldiers and workers of the Driver ants of West Africa, "they graduate insensibly into each other" alike in their sizes and in their structures; and that Professor Weismann's hypothesis implies a special set of "determinants" for each intermediate form. Or if he should say that the intermediate forms result from mixtures of the determinants of the two extreme forms, there still remains the further difficulty that natural selection has maintained, for innumerable generations, these intermediate forms which are injurious deviations from the useful extreme forms.

No reply.

One further reason—fatal it seems to me—was urged in bar of his interpretation. No physical cause has been, or can be, assigned, why in the germ-plasm of any particular queen-ant, the "determinants" initiating these various co-operative organs, all simultaneously vary in fitting ways and degrees, and still less why there occur such co-ordinated variations generation after generation, until, by their accumulated results, these efficient co-operative structures have been evolved. I pointed out that in the absence of any assigned or assignable physical cause, it is necessary to assume a fortuitous concurrence of favourable variations, which means "a fortuitous concourse of atoms"; and that it would be just as rational, and much more consistent, to assume that the structure of the entire organism thus resulted.

No reply.

It is reasonable to suspect that Professor Weismann recognized these difficulties as insuperable, for, in his Romanes Lecture on "The Effect of External Influences upon Development," instead of his previous indirect reply, he makes a direct reply. Reverting to the stag and its enlarging horns, he alleges a process by which, as he thinks, we may understand how, by variation and selection, all the bones and muscles of the neck, of the thorax, and of the fore-legs, are step by step adjusted in their sizes to the increasing sizes of the horns. He ascribes this harmonization to the internal struggle for nutriment, and that survival of the fittest which takes place among the parts of an organism: a process which he calls "*intra-individual*-selection, or more briefly—*intra-selection*" (p. 12).

"Wilhelm Roux has given an explanation of the cause of these wonderfully fine adaptations by applying the principle of selection to the parts of the organism. Just as there is a struggle for survival among the individuals of a species, and the fittest are victorious, so also do even the smallest living particles contend with one another, and those that succeed best in securing food and place grow and multiply rapidly, and so displace those that are less suitably equipped" (p. 12).*

That I do not explain as he does the co-adaptation of

* Prof. Weismann is unaware that the view here ascribed to Roux, writing in 1881, is of far earlier date. In the *Westminster Review* for January 1860, in an essay on "The Social Organism," I wrote:—"One more parallelism to be here noted, is that the different parts of a social organism, like the different parts of an individual organism, compete for nutriment; and severally obtain more or less of it according as they are discharging more or less duty." (See also *Essays*, i. 290.) And then, in 1876, in *The Principles of Sociology*, vol. i. § 247, I amplified the statement thus:—"All other organs, therefore, jointly and individually, compete for blood with each organ . . . local tissue-formation (which under normal conditions measures the waste of tissue in discharging function) is itself a cause of increased supply of materials . . . the resulting competition, not between units simply, but between organs, causes in a society, as in a living body, high nutrition and growth of parts called into greatest activity by the requirements of the rest." Though I did not use the imposing phrase "intra-individual-selection," the process described is the same.

co-operative parts, Professor Weismann ascribes to my having overlooked this "principle of intra-selection"—an unlucky supposition, as we see. But I do not think that when recognizing it a generation ago, I should have seen its relevancy to the question at issue, had that issue then been raised, and I certainly do not see it now. Full reproduction of Professor Weismann's explanation is impracticable, for it occupies several pages, but here are the essential sentences from it:—

"The great significance of intra-selection appears to me not to depend on its producing structures that are directly transmissible, —it cannot do that,—but rather consists in its causing a development of the germ-structure, acquired by the selection of individuals, which will be suitable to varying conditions. . . . We may therefore say that intra-selection effects the adaptation of the individual to its chance developmental conditions,—the suiting of the hereditary primary constituents to fresh circumstances" (p. 16). . . . "But as the primary variations in the phyletic metamorphosis occurred little by little, the secondary adaptations would probably as a rule be able to keep pace with them. Time would thus be gained till, in the course of generations, by constant selection of those germs the primary constituents of which are best suited to one another, the greatest possible degree of harmony may be reached, and consequently a definitive metamorphosis of the species involving all the parts of the individual may occur" (p. 19).

The connecting sentences, along with those which precede and succeed, would not, if quoted, give to the reader clearer conceptions than these by themselves give. But when disentangled from Professor Weismann's involved statements, the essential issues are, I think, clear enough. In the case of the stag, that daily working together of the numerous nerves, muscles and bones concerned, by which they are adjusted to the carrying and using of somewhat heavier horns, produces on them effects which, as I hold, are inheritable, but which, as Professor Weismann holds, are not inheritable. If they are not inheritable, what must happen? A fawn of the next generation is born with no such adjustment of nerves, muscles and bones as had been produced by greater exercise in the parent, and with no tendency to such adjustment. Consequently if, in successive generations, the horns go on enlarging, all these nerves, muscles and bones, remaining of the original sizes, become utterly inadequate. The result is loss of life: the process of adaptation fails. "No," says Professor Weismann, "we must conclude that the germ-plasm has varied in the needful manner." How so? The process of "intra-individual-selection," as he calls it, can have had no effect, since the cells of the soma cannot influence the reproductive cells. In what way, then, has the germ-plasm gained the characters required for producing simultaneously all these modified co-operative parts. Well, Professor Weismann tells us merely that we must suppose that the germ-plasm acquires a certain sensitiveness such as gives it a proclivity to development in the requisite ways. How is such proclivity obtainable? Only by having a multitude of its "determinants" simultaneously changed in fit modes. Emphasizing the fact that even a small failure in any one of the co-operative parts may be fatal, as the sprain of an over-taxed muscle shows us, I alleged that the chances are infinity to one against the needful variations taking place at the same time. Divested of its elaboration, its abstract words and technical phrases, the outcome of Professor Weismann's explanation is that he accepts this, and asserts that the infinitely improbable thing takes place!

Either his argument is a disguised admission of the inheritableness of acquired characters (the effects of "intra-selection") or else it is, as before, the assumption of a fortuitous concourse of favourable variations in the determinants —"a fortuitous concourse of atoms."

Leaving here this main issue, I return now to that collateral issue named on a preceding page as being postponed—whether the neuters among social insects result from specially modified germ-plasms or whether they result from the treatment received during their larval stages.

For the substantiation of his doctrine Professor Weismann is obliged to adopt the first of these alternatives; and in his Romanes Lecture he found it needful to deal with the evidence I brought in support of the second alternative. He says that "poor feeding is not the *causa efficiens* of sterility among bees, but is merely the stimulus which *not only results in the formation of rudimentary ovaries, but at the same time calls forth all the other distinctive characters of the workers*" (pp. 29–30); and he says this although he has in preceding lines admitted that it is "true of all animals that they reproduce only feebly or not at all when badly and insufficiently nourished:" a known cause being thus displaced by a supposed cause. But Professor Weismann proceeds to justify his interpretation by experimentally-obtained evidence.

He "reared large numbers of the eggs of a female blow-fly"; the larvæ of some he fed abundantly, but the larvæ of others sparingly; and eventually he obtained from the one set flies of full size, and from the other small flies. Nevertheless the small flies were fertile, as well as the others. Here, then, was proof that innutrition had not produced infertility; and he contends that therefore among the neuter social insects, infertility has not resulted from innutrition. The argument seems strong, and to many will appear conclusive; but there are two differences which entirely vitiate the comparison Professor Weismann institutes.

One of them has been pointed out by Mr. Cunningham. In the case of the blow-fly the food supplied to the larvæ though different in quantity was the same in quality; in the case of the social insects the food supplied, whether or not different in quantity, differs in quality. Among bees, wasps, ants, &c., the larvæ of the reproductive forms are fed upon a more nitrogenous food than are the larvæ of the workers; whereas the two sets of larvæ of the blow-fly, as fed by Professor Weismann, were alike supplied with highly nitrogenous food. Hence there did not exist the same cause for non-development of the reproductive organs. Here, then, is one vitiation of the supposed parallel. There is a second.

While the development of an embryo follows in a rude way the phyletic metamorphoses passed through by its ancestry, the order of development of organs is often gradually modified by the needs of particular species: the structures being developed in such order as conduces to self-sustentation and the welfare of offspring. Among other results there arise differences in the relative dates of maturity of the reproductive system and of the other systems. It is clear, *à priori*, that it must be fatal to a species if offspring are habitually produced before the conditions requisite for their survival are fulfilled. And hence, if the life is a complex one, and the care taken of offspring is great, reproduction must be much longer delayed than where the life is simple and the care of offspring absent or easy. The contrast between men and oxen sufficiently illustrates this truth. Now the subordination of the order of development of parts to the needs of the species, is conspicuously shown in the contrast between these two kinds of insects which Professor Weismann compares as though their requirements were similar. What happens with the blow-fly? If it is able to suck up some nutriment, to fly tolerably, and to scent out dead flesh, various of its minor organs may be more or less imperfect without appreciable detriment to the species: the eggs can be laid in a fit place, and that is all that is wanted. Hence it profits the species to have the reproductive system developed comparatively early —in advance, even, of various less essential parts. Quite otherwise is it with social insects, which take such remarkable care of their young; or rather, to make the case parallel —quite otherwise is it with those types from which the social insects have descended, bringing into the social state their inherited instincts and constitutions. Consider the doings of the mason-wasp, or mason-bee, or those of the carpenter-bee. What, in these cases, must the female do that she may rear members of the next generation? There is a fit place for building or burrowing to be chosen; there is the collecting together of grains of sand and cementing them into a strong and water-proof cell, or there is the burrowing into wood and there building several cells; there is the collecting of food to place along with the eggs deposited in these cells, solitary or associated, including that intelligent choice of small caterpillars which, discovered and carried home, are carefully packed away and hypnotized by a sting, so that they may live until the growing larva has need of them. For all these proceedings there have to be provided the fit external organs—cutting instruments, &c., and the fit internal organs—complicated nerve-centres in which are located these various remarkable instincts, and ganglia by which these delicate operations have to be guided. And these special structures have, some if not all of them, to be made perfect and brought into efficient action before egg-laying takes place. Ask what would happen if the reproductive system were active in advance of these ancillary appliances. The eggs would have to be laid without protection or food, and the species would forthwith disappear. And if that full development of the reproductive organs which is marked by their activity, is not needful until these ancillary organs have come into play, the implication, in conformity with the general law above indicated, is that the perfect development of the reproductive organs will take place later than that of these ancillary organs, and that if innutrition checks the general development, the reproductive organs will be those which chiefly suffer. Hence, in the social types which have descended from these solitary types, this order of evolution of parts will be inherited, and will entail the results I have inferred.

If only deductively reached, this conclusion would, I think, be fully justified. But now observe that it is more than deductively reached. It is established by observation. Professor Riley, Ph.D., late Government Entomologist of the United States, in his annual address as President of the Biological Society of Washington,* on January 29, 1894, said:—

* *Proceedings of the Biological Society of Washington*, vol. ix.

"Among the more curious facts connected with these Termites, because of their exceptional nature, is the late development of the internal sexual organs in the reproductive forms" (p. 34).

Though what has been shown of the Termites has not been shown of the other social insects, which belong to a different order, yet, considering the analogies between their social states and between their constitutional requirements, it is a fair inference that what holds in the one case holds partially, if not fully, in the other. Should it be said that the larval forms do not pass into the pupa-state in the one case as they do in the other, the answer is that this does not affect the principle. The larva carries into the pupa-state a fixed quantity of tissue-forming material for the production of the imago. If the material is sufficient, then a complete imago is formed. If it is not sufficient, then, while the earlier-formed organs are not affected by the deficiency, the deficiency is felt when the latest formed organs come to be developed, and they are consequently imperfect.

Even if left without reply, Professor Weismann's interpretation commits him to some insuperable difficulties, which I must now point out. Unquestionably he has "the courage of his opinions"; and it is shown throughout this collateral discussion as elsewhere. He is compelled by accumulated evidence to admit "that there is only *one* kind of egg, from which queens and workers as well as males arise."* But if the production of one or other form from the same germ does not result from speciality of feeding, what does it result from? Here is his reply:—

"We must rather suppose that the primary constituents of two distinct reproductive systems—*e.g.* those of the queen and worker—are contained in the germ-plasm of the egg." †

"The courage of his opinions," which Professor Weismann shows in this assumption, is, however, quite insufficient. For since he himself has just admitted that there is only one kind of egg for queens, workers, and males, he must at any rate assume three sets of "determinants." (I find that on a subse-

* Romanes Lecture, p. 29. † *Ib.* p. 35.

quent page he does so.) But this is not enough, for there are, in many cases, two if not more kinds of workers, which implies that four sets of determinants must co-exist in the same egg. Even now we have not got to the extent of the assumption required. In the address above referred to on "Social Insects from Psychical and Evolutional Points of View," Professor Riley gives us (p. 33) the—

Forms in a Termes Colony under Normal Conditions.

1. Youngest larvæ.

2. Larvæ [of those] unfit for reproduction. 3. Larvæ [that will be] fit for reproduction.

4. Larvæ of workers. 5. Larvæ of soldiers. 8. Nymphs of 1st form. 9. Nymphs of 2nd form.

6. Workers. 7. Soldiers. 10. Winged forms.

11. True royal pairs.

Hence as, in this family tree, the royal pair includes male and female, it results that there are *five* different adult forms (Grassi says there are two others) arising from like eggs or larvæ; and Professor Weismann's hypothesis becomes proportionately complicated. Let us observe what the complications are.

It often happens in controversy—metaphysical controversy more than any other—that propositions are accepted without their terms having been mentally represented. In public proceedings documents are often "taken as read," sometimes with mischievous results; and in discussions propositions are often taken as thought, when they have not been thought and cannot be thought. It sufficiently taxes imagination to assume, as Professor Weismann does, that two sets of "ids" or of "determinants" in the same egg are, throughout all the cell-divisions which end in the formation of the *morula*, kept separate, so that they may subsequently energize independently; or that if they are not thus kept separate, they have the power of segregating in the required ways. But what are we to say when three, four, and even five sets of "ids" or bundles of "determinants" are present? How is dichotomous division to keep these sets distinct; or if they are not kept distinct, what shall we say to the chaos which must arise after many fissions, when each set in conflict with the others strives to produce its particular structure? And how are the conquering determinants to find their ways out of the *mêlée* to the places where they are to fulfil their organizing functions? Even were they all intelligent beings and each had a map by which to guide his movements, the problem would be sufficiently puzzling. Can we assume it to be solved by unconscious units?

Thus even had Professor Weismann shown that the special structures of the different individuals in an insect-community are not due to differences in the nurtures they receive, which he has failed to do, he would still be met by this difficulty in the way of his own view, in addition to the three other insuperable difficulties grouped together in a preceding section.

The collateral issue, which has occupied the largest space in the controversy, has, as commonly happens, begotten a second generation of collateral issues. Some of these are embodied in the form of questions put to me, which I must here answer, lest it should be supposed that they are unanswerable and my view therefore untenable.

In the notes he appends to his Romanes Lecture, Professor Weismann writes:—

"One of the questions put to Spencer by Ball is quite sufficient to show the utter weakness of the position of Lamarckism:—if their characteristics did not arise among the workers themselves, but were transmitted from the pre-social time, how does it happen that the queens and drones of every generation can give anew to the workers the characteristics which they themselves have long ago lost?" (p. 68.)

It is curious to see put forward in so triumphant a manner, by a professed naturalist, a question so easily disposed of. I answer it by putting another. How does it happen that among those moths of which the female has but rudimentary wings, she continues to endow the males of her species with wings? How does it happen, for example, that among the *Geometridæ*, the peculiar structures and habits of which show that they have all descended from a common ancestor, some species have winged females and some wingless females; and that though they have lost the wings the ancestral females had, these wingless females convey to the males the normal developments of wings? Or, still better, how is it that in the *Psychidæ* there are apterous worm-like females, which lay eggs that bring forth winged males of the ordinary imago form? If for males we read workers, the case is parallel to the cases of those social insects, the queens of which bequeath characteristics they have themselves lost. The ordinary facts of embryonic evolution yield us analogies. What is the most common trait in the development of the sexes? When the sexual organs of either become pronounced, the incipient ancillary organs belonging to the opposite sex cease to develop and remain rudiments, while the organs special to the sex, essential and non-essential, become fully developed? What, then, must happen with the queen-ant, which, through countless generations, has ceased to use certain structures and has lost them from disuse? If one of the eggs which she lays, capable, as Professor Weismann admits, of becoming queen, male, or worker of one or other kind, does not at a certain stage begin actively to develop its reproductive system, then those organs of the ancestral or pre-social type which the queen has lost begin to develop, and a worker results.

Another difficulty in the way of my view, supposed to be fatal, is that presented by the Honey-ants—aberrant members of certain ant-colonies which develop so enormously the pouch into which the food is drawn, that the abdomen becomes little else than a great bladder out of which the head, thorax, and legs protrude. This, it is thought, cannot be accounted for otherwise than as a consequence of specially endowed eggs, which it has become profitable to the community for the queen to produce. But the explanation fits in quite easily with the view I have set forth. No one will deny that the taking in of food is the deepest of vital requirements, and the correlative instinct a dominant one; nor will any one deny that the instinct of feeding young is less deeply seated—comes later in order of time. So, too, every one will admit that the worker-bee or worker-ant before regurgitating food into the mouth of a larva must first of all take it in. Hence, alike in order of time and necessity, it is to be assumed that development of the nervous structures which guide self-nutrition, precedes development of the nervous structures which guide the feeding of larvæ. What, then, will in some cases happen, supposing there is an arrested development consequent on innutrition? It will in some cases happen that while the nervous centres prompting and regulating deglutition are fully formed, the formation of those prompting and regulating the regurgitation of the food into the mouths of larvæ are arrested. What will be the consequence? The life of the worker is mainly passed in taking in food and putting it out again. If the putting out is stopped its life will be mainly passed in taking in food. The receptacle will go on enlarging and it will eventually assume the monstrous form that we see.*

Here, however, to exclude misinterpretations, let me explain. I by no means deny that variation and selection have produced, in these insect-communities, certain effects such as Mr. Darwin suggested. Doubtless ant-queens vary; doubtless there are variations in their eggs; doubtless differences of structure in the resulting progeny sometimes prove advantageous to the stirp, and originate slight modifications of the species. But such changes, legitimately to be assumed, are changes in single parts—in single organs or portions of organs. Admission of this does not involve admission that

* This interpretation harmonizes with a fact which I learn from Prof. Riley, that there are gradations in this development, and that in some species the ordinary neuters swell their abdomens so greatly with food that they can hardly get home.

there can take place numerous correlated variations in different and often remote parts, which must take place simultaneously or else be useless. Assumption of this is what Professor Weismann's argument requires, and assumption of this we have seen to be absurd.

Before leaving the general problem presented by the social insects, let me remark that the various complexities of action not explained by inheritance from pre-social or semi-social types, are probably due to accumulated and transmitted knowledge. I recently read an account of the education of a butterfly, carried to the extent that it became quite friendly with its protector and would come to be fed. If a non-social and relatively unintelligent insect is capable of thus far consciously adjusting its actions, then it seems a reasonable supposition that in a community of social insects there has arisen a mass of experience and usage into which each new individual is initiated; just as happens among ourselves. We have only to consider the chaos which would result were we suddenly bereft of language, and if the young were left to grow up without precept and example, to see that very probably the polity of an insect-community is made possible by the addition of intelligence to instinct, and the transmission of information through sign-language.

There remains now the question of *panmixia*, which stands exactly where it did when I published the "Rejoinder to Professor Weismann."

After showing that the interpretation I put upon his view was justified by certain passages quoted; and after pointing out that one of his adherents had set forth the view which I combated—if not as his view yet as supplementary to it; I went on to criticize the view as set forth afresh by Professor Weismann himself. I showed that as thus set forth the actuality of the supposed cause of decrease in disused organs, implies that *minus* variations habitually exceed *plus* variations—in degree or in number, or in both. Unless it can be proved that such an excess ordinarily occurs, the hypothesis of *panmixia* has no place; and I asked, where is the proof that it occurs.

No reply.

Not content with this abstract form of the question I put it also in a concrete form, and granted for the nonce Professor Weismann's assumption: taking the case of the rudimentary hind limbs of the whale. I said that though, during those early stages of decrease in which the disused limbs were external, natural selection probably had a share in decreasing them, since they were then impediments to locomotion, yet when they became internal, and especially when they had dwindled to nothing but remnants of the femurs, it is impossible to suppose that natural selection played any part: no whale could have survived and initiated a more prosperous stirp in virtue of the economy achieved by such a decrease. The operation of natural selection being out of the question, I inquired whether such a decrease, say of one-half when the femurs weighed a few ounces, occurring in one individual, could be supposed in the ordinary course of reproduction to affect the whole of the whale species inhabiting the Arctic Seas and the North Atlantic Ocean; and so on with successive diminutions until the rudiments had reached their present minuteness. I asked whether such an interpretation could be rationally entertained.

No reply.

Now in the absence of replies to these two questions it seems to me that the verdict must go against Professor Weismann by default. If he has to surrender the hypothesis of *panmixia*, what results? All that evidence collected by Mr. Darwin and others, regarded by them as proof of the inheritance of acquired characters, which was cavalierly set aside on the strength of this alleged process of panmixia, is reinstated. And this reinstated evidence, joined with much evidence since furnished, suffices to establish the repudiated interpretation.

In the printed report of his Romanes Lecture, after fifty pages of complicated speculations which we are expected to accept as proofs, Professor Weismann ends by saying, in reference to the case of the neuter insects:—

This case is of additional interest, as it may serve to convince those naturalists who are still inclined to maintain that acquired characters are inherited, and to support the Lamarckian principle of development, that their view cannot be the right one. It has not proved tenable in a single instance (p. 54).

Most readers of the foregoing pages will think that since Professor Weismann has left one after another of my chief theses without reply, this is rather a strong assertion; and they will still further raise their eyebrows on remembering that, as I have shown, where he has given answers his answers are invalid.

And now we come to the additions which I indicated at the outset as having to be made—certain evidences which have come to light since this controversy commenced.

When, by a remembered observation made in boyhood, joined with the familiar fact that worker-larvæ can be changed into the larvæ of queens by feeding, I was led to suggest that probably all the variations of form in the social insects are consequent on differences of nurture, I was unaware that elaborate observations and experiments justifying this supposition had been made, and that Professor Grassi has recently published observations on the food-habits of two European species of Termites, shewing that the various forms are due to feeding. Professor Grassi is known to be a most careful observer, and some of the most curious of his facts are confirmed by the collection of white ants exhibited by Dr. David Sharp, F.R.S., at the *soirée* of the Royal Society in May last. He has favoured me with the following account of Grassi's results, which I publish with his assent:—

"There is great variety as to the constituents of the community and economy of the species in White Ants. One of the simplest conditions known is that studied by Grassi in the case of the European species Calotermes flavicollis. In this species there is no worker caste; the adult forms are only of two kinds, viz., soldiers, and the males and females; the sexes are externally almost indistinguishable, and there are males and females of soldiers as well as of the winged forms, though the sexual organs do not undergo their full development in any soldier whether male or female.

"The soldier is not however a mere instance of simple arrested development. It is true that there is in it arrested development of the sexual organs, but this is accompanied by change of form of other parts—changes so extreme that one would hardly suppose the soldier to have any connection with either the young or the adult of the winged forms.

"Now according to Grassi the whole of the individuals when born are undifferentiated forms (except as to sex), and each one is capable of going on the natural course of development and thus becoming a winged insect, or can be deviated from this course and made into a soldier; this is accomplished by the White Ants by special courses of feeding.

"The evidence given by Grassi is not conclusive as to the young being all born alike; and it may be that there are some individuals born that could not be deviated from the natural course and made into soldiers. But there is one case which seems to show positively that the deviation Grassi believes to occur is real, and not due to the selection by the ants of an individual that though appearing to our eyes undifferentiated is not really so. This is that an individual can be made into a soldier after it has visibly undergone one half or more of the development into a winged form. The Termites can in fact operate on an individual that has already acquired the rudiments of wings and whose head is totally destitute of any appearance of the shape or of the armature peculiar to the soldier, and can turn it into a soldier; the rudiments of the wings being in such a case nearly entirely reabsorbed."

Grassi has been for many years engaged in investigating these phenomena, and there is no reason for rejecting his statement. We can scarcely avoid accepting it, and if so, Professor Weismann's hypothesis is conclusively disposed of. Were there different sets of "determinants" for the soldier-form and for the winged sexual form, those "determinants" which had gone a long way towards producing the winged sexual form, would inevitably go on to complete that form, and could not have their proclivity changed by feeding.

The other piece of additional evidence I have referred to, is furnished by two papers contributed to *The Journal of*

Anatomy and Physiology for October 1893 and April 1894, by R. Havelock Charles, M.D., &c. &c., Professor of Anatomy in the Medical College, Lahore. These papers set forth the differences between the leg-bones of Europeans and those of the Punjaub people—differences caused by their respective habits of sitting in chairs and squatting on the ground. He enumerates more than twenty such differences, chiefly in the structures of the knee-joint and ankle-joint. From the *resumé* of his second paper I quote the following passages, which sufficiently show the data and the inferences:—

"7. The habits as to sitting postures of Europeans differ from those of their pre-historic ancestors, the Cave-dwellers, &c., who probably squatted on the ground.

"8. The sitting postures of Orientals are the same now as ever. They have retained the habits of their ancestors. The Europeans have not done so.

"9. Want of use would induce changes in form and size, and so, gradually, small differences would be integrated till there would be total disappearance of the markings on the European skeleton, as no advantage would accrue to him from the possession of facets on his bones fitting them for postures not practised by him.

10. "The facets seen on the bones of the Panjabi infant or fœtus have been transmitted to it by the accumulation of peculiarities gained by habit in the evolution of its racial type—in which an acquisition having become a permanent possession, 'profitable to the individual under its conditions of life,' is transmitted as a useful inheritance.

11. "These markings are due to the influence of certain positions, which are brought about by the use of groups of muscles, and they are the definite results produced by actions of these muscles.

12. "The effects of the use of the muscles mentioned in No. 11 are transmitted to the offspring, for the markings are present in the *fœtus-in-utero*, in the child at birth, and in the infant.

13. "The markings are instances of the transmission of acquired characters, which heritage in the individual, function subsequently develops."

No other conclusion appears to me possible. Panmixia, even were it not invalidated by its unwarranted assumption as above shown, would be out of court: the case is not a case of either increase or decrease of size but of numerous changes of form. Simultaneous variation of co-operative parts cannot be alleged, since these co-operative parts have not changed in one way but in various ways and degrees. And even were it permissible to suppose that the required different variations had taken place simultaneously, natural selection cannot be supposed to have operated. The assumption would imply that in the struggle for existence, individuals of the European races who were less capable than others of crouching and squatting, gained by those minute changes of structure which incapacitated them, such advantages that their stirps prevailed over other stirps—an absurd supposition.

And now I must once more point out that a grave responsibility rests on biologists in respect of the general question; since wrong answers lead, among other effects, to wrong beliefs about social affairs and to disastrous social actions. In me this conviction has unceasingly strengthened. Though *The Origin of Species* proved to me that the transmission of acquired characters cannot be the sole factor in organic evolution, as I had assumed in *Social Statics* and in *The Principles of Psychology*, published in pre-Darwinian days, yet I have never wavered in the belief that it is *a* factor and an all-important factor. And I have felt more and more that since all the higher sciences are dependent on the science of life, and must have their conclusions vitiated if a fundamental datum given to them by the teachers of this science is erroneous, it behoves these teachers not to let an erroneous datum pass current: they are called on to settle this vexed question one way or other. The times give proof. The work of Mr. Benjamin Kidd on *Social Evolution*, which has been so much lauded, takes Weismannism as one of its data; and if Weismannism be untrue, the conclusions Mr. Kidd draws must be in large measure erroneous and may prove mischievous.

[*See over.*

POSTSCRIPT.—Since the foregoing pages have been put in type there has appeared in *Natural Science* for September, an abstract of certain parts of a pamphlet by Professor Oscar Hertwig, setting forth facts directly bearing on Professor Weismann's doctrine respecting the distinction between reproductive cells and somatic cells. In *The Principles of Biology*, § 77, I contended that reproductive cells differ from other cells composing the organism, only in being unspecialized. And in support of the hypothesis that tissue-cells in general have a reproductive potentiality, I instanced the cases of the *Begonia phyllomaniaca* and *Malaxis paludosa*. In the thirty years which have since elapsed, many facts of like significance have been brought to light, and various of these are given by Professor Hertwig. Here are some of them :—

"Galls are produced under the stimulus of the insect almost anywhere on the surface of a plant. Yet in most cases these galls, in a sense grown at random on the surface of a plant, when placed in damp earth will give rise to a young plant. In the hydroid *Tubularia mesembryanthemum*, when the polyp-heads are cut off, new heads arise. But if both head and root be cut off, and the upper end be inserted in the mud, then from the original upper end not head-polyps but root filaments will arise, while from the original lower end not root filaments but head-polyps will grow. . . . Driesch, by separating the first two and the first four segmentation-spheres of an *Echinus* ovum, obtained two or four normal plutei, respectively one half and a quarter of the normal size. . . . So, also, in the case of *Amphioxus*, Wilson obtained a normal, but proportionately diminished, embryo with complete nervous system from a separated sphere of a two- or four- or eight-celled stage. . . . Chabry obtained normal embryos in cases where some of the segmentation-spheres had been artificially destroyed."

These evidences, furnished by independent observers, unite in showing, firstly, that all the multiplying cells of the developing embryo are alike; and, secondly, that the soma-cells of the adult severally retain, in a latent form, all the powers of the original embryo-cell. If these facts do not disprove absolutely Professor Weismann's hypothesis, we may wonderingly ask what facts would disprove it?

Since Hertwig holds that all the cells forming an organism of any species primarily consist of the same components, I at first thought that his hypothesis was identical with my own hypothesis of "physiological units," or, as I would now call them, constitutional units. It seems otherwise, however; for he thinks that each cell contains "only those material particles which are bearers of cell-properties," and that organs "are the functions of cell-complexes." To this it may be replied that the ability to form the appropriate cell-complexes, itself depends upon the constitutional units contained in the cells.

BALLANTYNE PRESS: LONDON.

10

A REJOINDER

TO

PROFESSOR WEISMANN

BY

HERBERT SPENCER

REPRINTED FROM *The Contemporary Review*

WILLIAMS & NORGATE

14 HENRIETTA STREET, COVENT GARDEN, LONDON

NOTE.

THE motives which have prompted me to reprint and distribute the following article from *The Contemporary Review* for December, 1893; are two.

The first, of course, is the desire to meet, not only in England but elsewhere, the arguments which Prof. Weismann has urged against my criticisms on his doctrines.

Beyond this special motive there is a more general one. In the course of the discussion, I have been led to set forth certain views concerning the origin and economy of the social insects, which differ from those that are current; and since they bear upon sundry biological questions of interest, it has seemed to me desirable to make them known more widely than they would be if limited to the pages of an English periodical.

I am, as before, obliged to the Editor of *The Contemporary Review* for agreeing to so early a republication.

H. S.

5 THE MOUNT.
ST. LEONARDS-ON-SEA,
Dec. 1893.

A

REJOINDER TO PROFESSOR WEISMANN.

As a species of literature, controversy is characterised by a terrible fertility. Each proposition becomes the parent of half a dozen; so that a few replies and rejoinders produce an unmanageable population of issues, old and new, which end in being a nuisance to everybody. Remembering this, I shall refrain from dealing with all the points of Professor Weismann's answer. I must limit myself to a part; and that there may be no suspicion of a selection convenient to myself, I will take those contained in his first article.

Before dealing with his special arguments, let me say something about the general mode of argument which Professor Weismann adopts.

The title of his article is "The All-Sufficiency of Natural Selection."* Very soon, however, as on p. 322, we come to the admission, which he has himself italicised, "that *it is really very difficult to imagine this process of natural selection in its details;* and to this day it is impossible to demonstrate it in any one point." Elsewhere, as on pp. 327 and 336 *à propos* of other cases, there are like admissions. But now if the sufficiency of an assigned cause cannot in any case be

* *Contemporary Review*, September 1893.

demonstrated, and if it is "really very difficult to imagine" in what way it has produced its alleged effects, what becomes of the "all-sufficiency" of the cause? How can its all-sufficiency be alleged when its action can neither be demonstrated nor easily imagined? Evidently to fit Professor Weismann's argument the title of the article should have been "The Doubtful Sufficiency of Natural Selection."

Observe, again, how entirely opposite are the ways in which he treats his own interpretation and the antagonist interpretation. He takes the problem presented by certain beautifully adapted structures on the anterior legs of "very many insects," which they use for cleansing their antennæ. These, he argues, cannot have resulted from the inheritance of acquired characters; since any supposed changes produced by function would be changes in the chitinous exo-skeleton, which, being a dead substance, cannot have had its changes transmitted. He then proceeds, very candidly, to point out the extreme difficulties which lie in the way of supposing these structures to have resulted from natural selection: admitting that an opponent might "say that it was absurd" to assume that the successive small variations implied were severally life-saving in their effects. Nevertheless, he holds it unquestionable that natural selection has been the cause. See then the difference. The supposition that the apparatus has been produced by the inheritance of acquired characters is rejected *because* it presents insuperable difficulties. But the supposition that the apparatus has been produced by natural selection is accepted, *though* it presents insuperable difficulties. If this mode of reasoning is allowable, no fair comparison between diverse hypotheses can be made.

With these remarks on Professor Weismann's method at large, let me now pass to the particular arguments he uses, taking them *seriatim*.

The first case he deals with is that of the progressive degradation of the human little toe. This he considers a good test case; and he proceeds to discuss an assigned cause—the inherited and accumulated effects of boot-pressure. Without much difficulty he shows that this interpretation is inadequate; since fusion of the phalanges, which constitutes in part the progressive degradation, is found among peoples who go barefoot, and has been found also in Egyptian mummies. Having thus disposed of Mr. Buckman's interpretation, Professor Weismann forthwith concludes that the ascription of this anatomical change to the inheritance of acquired characters is disposed of, and assumes, as the only other possible interpretation, a dwindling "through panmixia": "the hereditary degeneration of the little toe is thus quite simply explained from my standpoint."

It is surprising that Professor Weismann should not have seen that there is an explanation against which his criticism does not tell. If we go back to the genesis of the human type from some lower type of *primates*, we see that while the little toe has ceased to be of any use for climbing purposes, it has not come into any considerable use for walking and running. A glance at the feet of the sub-human *primates* in general, shows that the inner digits are, as compared with those of men, quite small—have no such relative length and massiveness as the human great toes. Leaving out the question of cause, it is manifest that the great toes have been immensely developed, since there took place the change from arboreal habits to terrestrial habits. A study of the mechanics of walking shows why this has happened Stability requires that the "line of direction" (the vertical line let fall from the centre of gravity) shall fall within the base, and, in walking, shall be brought at each step within the area of support, or so near it that any tendency to fall may be checked at the next step. A necessary result is that if, at each step, the chief stress of support is thrown on the outer side of the foot, the body must be swayed so that the "line of direction" may fall within the outer side of the foot, or close to it; and when the next step is taken it must be similarly swayed in an opposite way, so that the outer side of the other foot may bear the weight. That is to say, the body must oscillate from side to side, or waddle. The movements of a duck when walking or running show what happens when the points of support are wide apart. Clearly this kind of movement conflicts with efficient locomotion. There is a waste of muscular energy in making these lateral movements, and they are at variance with the forward movement. We may infer, then, that the developing man profited by throwing the stress as much as possible on the inner sides of the feet; and was especially led to do this when going fast, which enabled him to abridge the oscillations: as indeed we now see in a drunken man. Thus there was thrown a continually increasing stress upon the inner digits as they progressively developed from the effects of use; until now that the inner digits, so large compared with the others, bear the greater part of the weight, and being relatively near one another, render needless any marked swayings from side to side. But what has meanwhile happened to the outer digits? Evidently as fast as the great toes have come more and more into play and developed, the little toes have gone more and more out of play and have been dwindling for—how long shall we say?—perhaps a hundred thousand years.

So far then am I from feeling that Professor Weismann has here raised a difficulty in the way of the doctrine I hold, that I feel indebted to him for having drawn attention to a very strong evidence in its support. This modification in the form of the foot, which has occurred since arboreal habits have given place to terrestrial habits, shows the effects of use and disuse simultaneously. The inner digits have increased by use while the outer digits have decreased by disuse.

Saying that he will not "pause to refute other apparent proofs of the transmission of acquired characters," Professor

Weismann proceeds to deal with the argument which, with various illustrations, I have several times urged—the argument that the natural selection of fortuitously-arising variations cannot account for the adjustment of co-operative parts. Very clearly and very fairly he summarises this argument as used in *The Principles of Biology* in 1864. Admitting that in this case there are "enormous difficulties" in the way of any other interpretation than the inheritance of acquired characters, Professor Weismann before proceeding to assault this "last bulwark of the Lamarckian principle," premises that the inheritance of acquired characters cannot be a cause of change because inactive as well as active parts degenerate when they cease to be of use: instancing the "skin and skin-armature of crabs and insects." On this I may remark in the first place that an argument derived from degeneracy of passive structures scarcely meets the case of development of active structures; and I may remark in the second place that I have never dreamt of denying the efficiency of natural selection as a cause of degeneracy in passive structures when the degeneracy is such as aids the prosperity of the stirp.

Making this parenthetical reply to his parenthetical criticism I pass to his discussion of this particular argument which he undertakes to dispose of.

His *cheval de bataille* is furnished him by the social insects —not a fresh one, however, as might be supposed from the way in which he mounts it. From time to time it has carried other riders, who have couched their lances with fatal effects as they supposed. But I hope to show that no one of them has unhorsed an antagonist, and that Professor Weismann fails to do this just as completely as his predecessors. I am, indeed, not sorry that he has afforded me the opportunity of criticising the general discussion concerning the peculiarities of these interesting creatures, which it has often seemed to me sets out with illegitimate assumptions. The supposition always is that the specialities of structures and instincts in the unlike classes of their communities, have arisen during the period in which the communities have existed in something like their present forms. This cannot be. It is doubtless true that association without differentiations of classes may pre-exist for co-operative purposes, as among wolves, and as among various insects which swarm under certain circumstances. Hence we may suppose that there arise in some cases permanent swarms—that survival of the fittest will establish these constant swarms where they are advantageous. But admitting this, we have also to admit a gradual rise of the associated state out of the solitary state. Wasps and bees present us with gradations. If then we are to understand how the organized societies have arisen, either out of the solitary state or out of undifferentiated swarms, we must assume that the differences of structure and instinct among the members of them arose little by little, as the social organization arose little by little. Fortunately we are able to trace the greater part of the process in the annually-formed communities of the common wasp; and we shall recognize in it an all-important factor (ignored by Professor Weismann) to which the phenomena, or at any rate the greater part of them, are due.

But before describing the wasp's annual history, let me set down certain observations made when, as a boy, I was given to angling, and, in July or August, sometimes used for bait "wasp-grubs," as they were called. After having had for two or three days the combs or "cakes" of these, full of unfed larvæ in all stages of growth, I often saw some of them devouring the edges of their cells to satisfy their appetites; and saw others, probably the most advanced in growth, which were spinning the little covering caps to their cells, in preparation for assuming the pupa state. It is to be inferred that if, after a certain stage of growth has been reached, the food-supply becomes inadequate or is stopped altogether, the larva undergoes its transformation prematurely; and, as we shall presently see, this premature transformation has several natural sequences.

Let us return now to the wasp's family history. In the spring, a queen-wasp or mother-wasp which has survived the winter, begins to make a small nest containing four or more cells in which she lays eggs, and as fast as she builds additional cells, she lays an egg in each. Presently, to these activities, is added the feeding of the larvæ: one result being that the multiplication of larvæ involves a restriction of the food that can be given to each. If we suppose that the mother-wasp rears no more larvæ than she can fully feed, there will result queens or mothers like herself, relatively few in number. But if we suppose that, laying more numerous eggs she produces more larvæ than she can fully feed, the result will be that when these have reached a certain stage of growth, inadequate supply of food will be followed by premature retirement and transformation into pupæ. What will be the characters of the developed insects? The first effect of arrested nutrition will be smaller size. This we find. A second effect will be defective development of parts that are latest formed and least important for the survival of the individual. Hence we may look for arrested development of the reproductive organs—non-essential to individual life. And this expectation is in accord with what we see in animal development at large; for (passing over entirely sexless individuals) we see that though the reproductive organs may be marked out early in the course of development, they are not made fit for action until after the structures for carrying on individual life are nearly complete. The implication is, then, that an inadequately-fed and small larva will become a sterile imago. Having noted this, let us pass to a remarkable concomitant. In the course of development, organs are formed not alone in the order of their original succession, but partly in the order of importance and the share they have to take in adult activities—a change of order called by Haeckel "heterochrony." Hence the fact that we often see the maternal instinct precede the sexual instinct. Every little girl with her doll shows us that the one may become alive while the other remains dormant. In the case of wasps, then, premature arrest of development may result in incompleteness of the sexual traits, along with completeness of the maternal traits. What happens? Leave out the laying of eggs, and the energies of the mother-wasp are spent wholly in building cells and feeding larvæ, and the worker-wasp forthwith begins to spend its life in building cells and feeding larvæ. Thus interpreting the facts, we have no occasion to assume any constitutional difference between the eggs of worker-wasps and the eggs of queens; and that their eggs are not different we see, first, in the fact that occasionally the worker-wasp is fertile and lays drone-producing eggs, and we see secondly that (if in this respect they are like the bees, of which, however, we have no proof) the larva of a worker-wasp can be changed into the larva of a queen-wasp by special feeding. But be this as it may, we have good evidence that the feeding determines everything. Says Dr. Ormerod, in his *British Social Wasps*:—

> "When the swarm is strong and food plentiful . . . the well fed larvæ develop into females, full, large, and overflowing with fat. There are all gradations of size, from the large fat female to the smallest worker. . . . . The larger the wasp, the larger and better developed, as the rule, are the female organs, in all their details. In the largest wasps, which are to be the queens of another year, the ovaries differ to all appearances in nothing but their size from those of the larger worker wasps. . . . . Small feeble swarms produce few or no perfect females; but in large strong swarms they are found by the score" (pp. 248–9).

To this evidence add the further evidence that queens and workers pass through certain parallel stages in respect of their maternal activities. At first the queen, besides laying eggs, builds cells and feeds larvæ, but after a time ceases to build cells, and feeds larvæ only, and eventually doing neither one nor the other, only lays eggs, and is supplied with food by the workers. So it is in part with the workers. While the members of each successive brood, when in full vigour, build cells and feed larvæ, by-and-by they cease to build cells, and only feed larvæ: the maternal activities and instincts undergo analogous changes. In this case, then, we are not obliged to assume that only by a process of natural selection can the differences of structure and instinct between queens and workers be produced. The only way in which natural selection here comes into play is in the better survival of the families of those queens which made as many cells, and laid as many eggs, as resulted in the best number of half-fed larvæ, producing workers; since by a rapid multiplication of workers the family is advantaged, and the ultimate production of more queens surviving into the next year insured.

The differentiation of classes does not go far among the wasps, because the cycle of processes is limited to a year, or rather to the few months of the summer. It goes further among the hive-bees, which, by storing food, survive from one year into the next. Unlike the queen-wasp, the queen-bee neither builds cells nor gathers food, but is fed by the workers: egg-laying has become her sole business. On the other hand the workers, occupied exclusively in building and nursing, have the reproductive organs more dwarfed than they are in wasps. Still we see that the worker-bee occasionally lays drone-producing eggs, and that, by giving extra nutriment and the required extra space, a worker-larva can be developed into a queen-larva. In respect to the leading traits, therefore, the same interpretation holds. Doubtless there are subsidiary instincts which are apparently not thus interpretable. But before it can be assumed that an interpretation of another kind is necessary, it must be shown that these instincts cannot be traced back to those pre-social types and semi-social types which must have preceded the social types we now see. For unquestionably existing bees must have brought with them from the pre-social state an extensive endowment of instincts, and, acquiring other instincts during the unorganized social state, must have brought these into the present organized social state. It is clear, for instance, that the cell-building instinct in all its elaboration was mainly developed in the pre-social stage; for the transition from species building solitary cells to those building combs is traceable. We are similarly enabled to account for swarming as being an inheritance from remote ancestral types. For just in the same way that, with underfeeding of larvæ, there result individuals with imperfectly developed reproductive systems, so there will result individuals with imperfect sexual instincts; and just as the imperfect reproductive system partially operates upon occasion, so will the imperfect sexual instinct. Whence it will result that on the event which causes a queen to undertake a nuptial flight, which is effectual, the workers may take abortive nuptial flights: so causing a swarm.

And here, before going further, let us note an instructive class of facts related to the class of facts above set forth. Summing up, in a chapter on "The Determination of Sex," an induction from many cases, Professor Geddes and Mr. Thompson remark that "such conditions as deficient or abnormal food," and others causing "preponderance of waste over repair . . . . tend to result in production of males;" while "abundant and rich nutrition" and other conditions which "favour constructive processes . . . . result in the production of females."* Among such evidences of this, as immediately concern us, are these:—J. H. Fabre found that in the nests of *Osmia tricornis*, eggs at the bottom, first laid, and accompanied by much food, produced females, while those at the top, last laid, and accompanied by one-half or one-third the quantity of food, produced males.† Huber's observations on egg-laying by the honey-bee, show that in the normal course of things, the queen lays eggs of workers for eleven months, and only then lays eggs of drones: that is, when declining nutrition or exhaustion has set in. Further,

* *Evolution of Sex*, p. 50.

† *Souvenirs Entomologiques*, 3me Série, p. 328.

we have the above-named fact, shown by wasps and bees, that when workers lay eggs these produce drones only.* Special evidence, harmonizing with general evidence, thus proves that among these social insects the sex is determined by degree of nutrition while the egg is being formed. See then how congruous this evidence is with the conclusion above drawn; for it is proved that after an egg, predetermined as a female, has been laid, the character of the produced insect as a perfect female or imperfect female is determined by the nutrition of the larva. *That is, one set of differences in structures and instincts is determined by nutrition before the egg is laid, and a further set of differences in structures and instincts is determined by nutrition after the egg is laid.*

We come now to the extreme case—that of the ants. Is it not probable that the process of differentiation has been similar? There are sundry reasons for thinking so. With ants as with wasps and bees—the workers occasionally lay eggs; and an ant-community can, like a bee-community, when need be, produce queens out of worker-larvæ: presumably in the same manner by extra feeding. But here we have to add special evidence of great significance. For observe that the very facts concerning ants, which Professor Weismann names as exemplifying the formation of the worker type by selection, serve, as in the case of wasps, to exemplify its formation by arrested nutrition. He says that in several species the egg-tubes in the ovaries show progressive decrease in number; and this, like the different degrees of arrest in the ovaries of the worker-wasps, indicates arrest of larva-feeding at different stages. He gives cases showing that, in different degrees, the eyes of workers are less developed in the number of their facets than those of the perfect insects; and he also refers to the wings of workers as not being developed: remarking, however, that the rudiments of their wings show that the ancestral forms had wings. Are not these traits also results of arrested nutrition? Generally

* *Natural History of Bees*, new ed. p. 33.

among insects the larvæ are either blind or have but rudimentary eyes; that is to say, visual organs are among the latest organs to arise in the genesis of the perfect organism. Hence early arrest of nutrition will stop formation of these, while various more ancient structures have become tolerably complete. Similarly with wings. Wings are late organs in insect phylogeny, and therefore will be among those most likely to abort where development is prematurely arrested. And both these traits will, for the same reason, naturally go along with arrested development of the reproductive system. Even more significant, however, is some evidence assigned by Mr. Darwin respecting the caste-gradations among the driver-ants of West Africa. He says:—

> "But the most important fact for us is, that, though the workers can be grouped into castes of different sizes, yet they graduate insensibly into each other, as does the widely-different structure of their jaws."*

"Graduate insensibly," he says; implying that there are very numerous intermediate forms. This is exactly what is to be expected if arrest of nutrition be the cause; for unless the ants have definite measures, enabling them to stop feeding at just the same stages, it must happen that the stoppage of feeding will be indefinite; and that, therefore, there will be all gradations between the extreme forms—"insensible gradations," both in size and in jaw-structure.

In contrast with this interpretation, consider now that of Professor Weismann. From whichever of the two possible suppositions he sets out, the result is equally fatal. If he is consistent, he must say that each of these intermediate forms of workers must have its special set of "determinants," causing its special set of modifications of organs; for he cannot assume that while perfect females and the extreme types of workers have their different sets of determinants, the intermediate types of workers have not. Hence we are introduced to the strange conclusion that

---

* *Origin of Species*, 6th ed. p. 232.

besides the markedly-distinguished sets of determinants there must be, to produce these intermediate forms, many other sets slightly distinguished from one another—a score or more kinds of germ-plasm in addition to the four chief kinds. Next comes an introduction to the still stranger conclusion, that these numerous kinds of germ-plasm, producing these numerous intermediate forms, are not simply needless but injurious—produce forms not well fitted for either of the functions discharged by the extreme forms: the implication being that natural selection has originated these disadvantageous forms! If to escape from this necessity for suicide, Professor Weismann accepts the inference that the differences among these numerous intermediate forms are caused by arrested feeding of the larvæ at different stages, then he is bound to admit that the differences between the extreme forms, and between these and perfect females, are similarly caused. But if he does this, what becomes of his hypothesis that the several castes are constitutionally distinct, and result from the operation of natural selection? Observe, too, that his theory does not even allow him to make this choice; for we have clear proof that unlikenesses among the forms of the same species cannot be determined this way or that way by differences of nutrition. English greyhounds and Scotch greyhounds do not differ from one another so much as do the Amazon-workers from the inferior workers, or the workers from the queens. But no matter how a pregnant Scotch greyhound is fed, or her pups after they are born, they cannot be changed into English greyhounds: the different germ-plasms assert themselves spite of all treatment. But in these social insects the different structures of queens and workers *are* determinable by differences of feeding. Therefore the production of their various castes does not result from the natural selection of varying germ-plasm.

Before dealing with Professor Weismann's crucial case—that co-adaptation of parts, which, in the soldier-ants, has, he thinks, arisen without inheritance of acquired characters—let me deal with an ancillary case which he puts forward as explicable by "panmixia alone." This is the "degeneration, in the warlike Amazon-ants, of the instinct to search for food."* Let us first ask what have been the probable antecedents of these Amazon-ants; for, as I have above said, it is absurd to speculate about the structures and instincts the species possesses in its existing organized social state without asking what structures and instincts it brought with it from its original solitary state and its unorganised social state. From the outset these ants were predatory. Some variety of them led to swarm—probably at the sexual season—did not again disperse so soon as other varieties. Those which thus kept together derived advantages from making simultaneous attacks on prey, and prospered accordingly. Of descendants the varieties which carried on longest the associated state prospered most; until, at length, the associated state became permanent. All which social progress took place while there existed only perfect males and females. What was the next step? Ants utilize other insects, and, among other ways of doing this, sometimes make their nests where there are useful insects ready to be utilized. Giving an account of certain New Zealand species of *Tetramorium*, Mr. W. W. Smith says they seek out underground places where there are "root-feeding aphides and coccids," which they begin to treat as domestic animals; and further he says that when, after the pairing season, new nests are being formed, there are "a few ants of both sexes . . . from two up to eight or ten."† Carrying with us this fact as a key, let us ask what habits will be fallen into by the conquering species of ants. They, too, will seek places where there are creatures to be utilized; and, finding it profitable, will invade the habitations not of defenceless creatures only, but of creatures whose powers of defence are inadequate—weaker species of their own order. A very small modification will affiliate their

* *Contemporary Review*, September 1893, p. 333.

† *The Entomologist's Monthly Magazine*, March 1892, p. 61.

habits on habits of their prototypes. Instead of being supplied with sweet substance excreted by the aphides they are supplied with sweet substance by the ants among which they parasitically settle themselves. How easily the subjugated ants may fall into the habit of feeding them, we shall see on remembering that already they feed not only larvæ but adults—individuals bigger than themselves. And that attentions kindred to these paid to parasitic ants may be established without difficulty, is shown us by the small birds which continue to feed a young cuckoo in their nest when it has outgrown them. This advanced form of parasitism grew up while there were yet only perfect males and females, as happens in the initial stage with these New Zealand ants. What further modifications of habits were probably then acquired? From the practice of settling themselves where there already exist colonies of aphides, which they carry about to suitable places in the nest, like *Tetramorium*, other ants pass to the practice of making excursions to get aphides, and putting them in better feeding places where they become more productive of saccharine matter. By a parallel step these soldier-ants pass from the stage of settling themselves among other ants which feed them, to the stage of fetching the pupæ of such ants to the nest: a transition like that which occurs among slave-making human beings. Thus by processes analogous to those we see going on, these communities of slave-making ants may be formed. And since the transition from an unorganized social state to a social state characterized by castes, must have been gradual, there must have been a long interval during which the perfect males and females of these conquering ants could acquire habits and transmit them to progeny. A small modification accounts for that seemingly-strange habit which Professor Weismann signalizes. For if, as is observed, those ants which keep aphides solicit them to excrete a supply of ant-food by stroking them with the antennæ, they come very near to doing that which Professor Weismann says the soldier-ants do towards a worker—"they come to it and beg for food:" the food being put into their mouths in this last case as almost or quite in the first. And evidently this habit of passively receiving food, continued through many generations of perfect males and females, may result in such disuse of the power of self-feeding that this is eventually lost. The behaviour of young birds, during, and after, their nest-life, gives us the clue. For a week or more after they are full-grown and fly about with their parents, they may be seen begging for food and making no efforts to recognize and pick up food for themselves. If, generation after generation, feeding of them in full measure continued, they would not learn to feed themselves: the perceptions and instincts implied in self-feeding would be later and later developed, until, with entire disuse of them, they would disappear altogether by inheritance. Thus self-feeding may readily have ceased among these soldier-ants before the caste-organisation arose among them.

With this interpretation compare the interpretation of Professor Weismann. I have before protested against arguing in abstracts without descending to concretes. Here let us ask what are the particular changes which the alleged explanation by survival of the fittest involves. Suppose we make the very liberal supposition that an ant's central ganglion bears to its body the same ratio as the human brain bears to the human body—say, one-fortieth of its weight. Assuming this, what shall we assume to be the weight of those ganglion-cells and fibres in which are localized the perceptions of food and the suggestion to take it? Shall we say that these amount to one-tenth of the central ganglion? This is a high estimate considering all the impressions which this ganglion has to receive and all the operations which it has to direct. Still we will say one-tenth. Then it follows that this portion of nervous substance is one–400th of the weight of its body. By what series of variations shall we say that it is reduced from full power to entire incapacity? Shall we say five? This is a small number to assume. Nevertheless we will assume it. What results? That the economy of nerve-substance achieved by each of these five variations will amount to one–2000th of the entire mass. Making these highly favourable assumptions, what follows? The queen-ant lays eggs that give origin to individuals in each of which there is achieved an economy in nerve-substance of one-2000th of its weight; and the implication of the hypothesis is that such an economy will so advantage this ant-community that in the competition with other ant-communities it will conquer. For here let me recall the truth before insisted upon, that natural selection can operate only on those variations which appreciably benefit the stirp. Bearing in mind this requirement, is any one now prepared to say that survival of the fittest can cause this decline of the self-feeding faculty? *

Not limiting himself to the Darwinian interpretation, however, Professor Weismann says that this degradation may be accounted for by "panmixia alone." Here I will not discuss the adequacy of this supposed cause, but will leave it to be dealt with by implication a few pages in advance, where the general hypothesis of panmixia will be reconsidered.

And now, at length, we are prepared for dealing with Professor Weismann's crucial case—with his alleged disproof that co-adaptation of co-operative parts results from inheritance of acquired characters, because, in the case of the Amazon-ants, it has arisen where the inheritance of acquired characters is impossible. For after what has been said, it will be manifest that the whole question is begged when it is assumed that this co-adaptation has arisen since there existed

* Perhaps it will be alleged that nerve-matter is costly, and that this minute economy might be of importance. Anyone who thinks this will no longer think it after contemplating a litter of half-a-dozen young rabbits (in the wild rabbit the number varies from four to eight); and on remembering that the nerve-matter contained in their brains and spinal cords, as well as the materials for building up the bones, muscles, and viscera of their bodies, has been supplied by the doe in the space of a month; at the same time that she has sustained herself and carried on her activities: all this being done on relatively poor food. Nerve-matter cannot be so very costly then.

among these ants an organized social state. Unquestionably this organized social state pre-supposes a series of modifications through which it has been reached. It follows, then, that there can be no rational interpretation without a preceding inquiry concerning that earlier state in which there were no castes, but only males and females. What kinds of individuals were the ancestral ants—at first solitary and then semi-social? They must have had marked powers of offence and defence. Of predacious creatures, it is the more powerful which form societies, not the weaker. Instance human races. Nations originate from the relatively warlike tribes, not from the relatively peaceful tribes. Among the several types of individuals forming the existing ant community, to which, then, did the ancestral ants bear the greatest resemblance? They could not have been like the queens, for these, now devoted to egg-laying, are unfitted for conquest. They could not have been like the inferior class of workers, for these, too, are inadequately armed and lack strength. Hence they must have been most like these Amazon ants or soldier-ants, which now make predatory excursions—which now do, in fact, what their remote ancestors did. What follows? Their co-adapted parts have not been produced by the selection of variations within the ant-community, such as we now see it. They have been inherited from the pre-social and early social types of ants, in which the co-adaptation of parts had been effected by inheritance of acquired characters. It is not that the soldier-ants have gained these traits; it is that the other castes have lost them. Early arrest of development causes absence of them in the inferior workers; and from the queens they have slowly disappeared by inheritance of the effects of disuse. For, in conformity with ordinary facts of development, we may conclude that in a larva which is being so fed as that the development of the reproductive organs is becoming pronounced, there will simultaneously commence arrest in the development of those organs which are not to be used. There are abundant proofs that along with rapid growth of some organs others abort. And if these inferences are true, then Professor Weismann's argument falls to the ground. Nay, it falls to the ground even if conclusions so definite as these be not insisted upon; for before he can get a basis for his argument he must give good reasons for concluding that these traits of the Amazon-ants have *not* been inherited from remote ancestors.

One more step remains. Let us grant him his basis, and let us pass from the above negative criticism to a positive criticism. As before, I decline to follow the practice of talking in abstracts instead of in concretes, and contend that, difficult as it may be to see how natural selection has in all cases operated, we ought, at any rate, to trace out its operation whenever we can, and see where the hypothesis lands us. According to Prof. Weismann's admission, for production of the Amazon-ant by natural selection "*many parts must have varied simultaneously and in harmony with one another*"; * and he names as such, larger jaws, muscles to move them, larger head, and thicker chitin for it, bigger nerves for the muscles, bigger motor centres in the brain, and, for the support of the big head, strengthening of the thorax, limbs, and skeleton generally. As he admits, all these parts must have varied simultaneously in due proportion to one another, What must have been the proximate causes of their variations? They must have been variations in what he calls the "determinants." He says:—

"We have, however, to deal with the transmission of parts which are *variable* and this necessitates the assumption that just as many independent and variable parts exist in the germ-plasm as are present in the fully formed organism." †

Consequently to produce simultaneously these many variations of parts, adjusted in their sizes and shapes, there must have simultaneously arisen a set of corresponding variations in the "determinants" composing the germ-plasm. What made them simultaneously vary in the requisite ways? Pro-

* *Loc. cit.* p. 318. † *The Germ Plasm*, p. 54.

fessor Weismann will not say that there was somewhere a foregone intention. This would imply supernatural agency. He makes no attempt to assign a physical cause for these simultaneous appropriate variations in the determinants: an adequate physical cause being inconceivable. What, then, remains as the only possible interpretation? Nothing but *a fortuitous concourse of variations*; reminding us of the old "fortuitous concourse of atoms." Nay, indeed, it is the very same thing. For each of the "determinants," made up of "biophors," and these again of protein-molecules, and these again of simpler chemical molecules, must have had its molecular constitution changed in the required way; and the molecular constitutions of all the "determinants," severally modified differently, but in adjustment to one another, must have been thus modified by "a fortuitous concourse of atoms." Now if this is an allowable supposition in respect of the "determinants," and the varying organs arising from them, why is it not an allowable supposition in respect of the organism as a whole? Why not assume "a fortuitous concourse of atoms" in its broad, simple form? Nay, indeed, would not this be much the easier? For observe, this co-adaptation of numerous co-operative parts is not achieved by one set of variations, but is achieved gradually by a series of such sets. That is to say, the "fortuitous concourse of atoms" must have occurred time after time in appropriate ways. We have not one miracle, but a series of miracles!

Of the two remaining points in Professor Weismann's first article which demand notice, one concerns his reply to my argument drawn from the distribution of tactual discriminativeness. In what way does he treat this argument? He meets it by an argument derived from hypothetical evidence—not actual evidence. Taking the case of the tongue-tip, I have carefully inquired whether its extreme power of tactual discrimination can give any life-saving advantage in moving about the food during mastication, in detecting foreign bodies in it, or for purposes of speech; and have, I think, shown that the ability to distinguish between points one twenty-fourth of an inch apart is useless for such purposes. Professor Weismann thinks he disposes of this by observing that among the apes the tongue is used as an organ of touch. But surely a counter-argument equivalent in weight to mine should have given a case in which power to discriminate between points one twenty-fourth of an inch apart instead of one-twentieth of an inch apart (a variation of one-sixth) had a life-saving efficacy; or, at any rate, should have suggested such a case. Nothing of the kind is done or even attempted. But now note that his reply, accepted even as it stands, is suicidal. For what has the trusted process of panmixia been doing ever since the human being began to evolve from the ape? Why during thousands of generations has not the nervous structure giving this extreme discriminativeness dwindled away? Even supposing it had been proved of life-saving efficacy to our simian ancestors, it ought, acccording to Professor Weismann's own hypothesis to have disappeared in us. Either there was none of the assumed special capacity in the ape's tongue, in which case his reply fails, or panmixia has not operated, in which case his theory of degeneracy fails.

All this, however, is but preface to the chief answer. The argument drawn from the case of the tongue-tip, with which alone Professor Weismann deals, is but a small part of my argument, the remainder of which he does not attempt to touch—does not even mention. Had I never referred to the tongue-tip at all, the various contrasts in discriminativeness which I have named, between the one extreme of the forefinger-tip and the other extreme of the middle of the back, would have abundantly sufficed to establish my case—would have sufficed to show the inadequacy of natural selection as a key and the adequacy of the inheritance of acquired characters.

It seems to me, then, that judgment must go against him by default. Practically he leaves the matter standing just where it did.*

The other remaining point concerns the vexed question of panmixia. Confirming the statement of Dr. Romanes, Professor Weismann says that I have misunderstood him. Already (*Contemporary Review*, May 1893, p. 758, and Reprint, p. 66) I have quoted passages which appeared to justify my interpretation, arrived at after much seeking. Already, too, in this review (July, 1893, p. 54) I have said why I did

---

* While Professor Weismann has not dealt with my argument derived from the distribution of discriminativeness on the skin, it has been criticized by Mr. McKeen Cattell, in the last number of *Mind* (October 1893). His general argument, vitiated by extreme misconceptions, I need not deal with. He says:—"Whether changes acquired by the individual are hereditary, and if so to what extent, is a question of great interest for ethics no less than for biology. But Mr. Spencer's application of this doctrine to account for the origin of species [!] simply begs the question. He assumes useful variations [!]—whether of structure or habit is immaterial —without attempting to explain their origin." The only part of Mr. Cattell's criticism requiring reply is that which concerns the "sensation-areas" on the skin. He implies that since Weber, experimental psychologists have practically set aside the theory of sensation-areas: showing, among other things, that relatively great accuracy of discrimination can be quickly acquired by "increased interest and attention. . . . Practice for a few minutes will double the accuracy of discrimination, and practice on one side of the body is carried over to the other." To me it seems manifest that "increased interest and attention" will not enable a patient to discriminate two points where a few minutes before he could perceive only one. That which he can really do in this short time is to learn to discriminate between the *massiveness of a sensation* produced by two points and the massiveness of that produced by one, and to *infer* one point or two points accordingly. Respecting the existence of sensation-areas marked off from one another, I may, in the first place, remark that since the eye originates as a dermal sac, and since its retina is a highly developed part of the sensitive surface at large, and since the discriminative power of the retina depends on the division of it into numerous rods and cones, each of which gives a separate sensation-area, it would be strange were the discriminative power of the skin at large achieved by mechanism fundamentally different. In the second place I may remark that if Mr. Cattell will refer to Professor Karl Retzius's *Biologische Untersuchungen*, New Series,

not hit upon the interpretation now said to be the true one: I never supposed that any one would assume, without assigned cause, that (apart from excluded influence of disuse) the *minus* variations of a disused organ are greater than the *plus* variations. This was a tacit challenge to produce reasons for the assumption. Professor Weismann does not accept the challenge, but simply says:—"In my opinion all organs are maintained at the height of their development only through uninterrupted selection" (p. 332): in the absence of which they decline. Now it is doubtless true that as a naturalist he may claim for his "opinion" a relatively great weight. Still, in pursuance of the methods of science, it seems to me that something more than an opinion is required as the basis of a far-reaching theory.*

---

vol. iv. (Stockholm, 1892), he will see elaborate diagrams of superficial nerve-endings in various animals showing many degrees of separateness. I guarded myself against being supposed to think that the sensation-areas are sharply marked off from one another; and suggested, contrariwise, that probably the branching nerve-terminations intruded among the branches of adjacent nerve-terminations. Here let me add that the intrusion may vary greatly in extent; and that where the intruding fibres run far among those of adjacent areas, the discriminativeness will be but small, while it will be great in proportion as each set of branching fibres is restricted more nearly to its own area. All the facts are explicable on this supposition.

* Though Professor Weismann does not take up the challenge, Dr. Romanes does. He says:—"When selection is withdrawn there will be no excessive *plus* variations, because so long as selection was present the efficiency of the organ was maintained at its highest level: it was only the *minus* variations which were then eliminated." (*Contemporary Review*, p. 611.) In the first place, it seems to me that the phrases used in this sentence beg the question. It says that "the efficiency of the organ was maintained at its *highest* level"; which implies that the highest level is the best and that the tendency is to fall below it. This is the very thing I ask proof of. Suppose I invert the idea and say that the organ is maintained at its right size by natural selection, because this prevents increase beyond the size which is best for the organism. Every organ should be in due proportion, and the welfare of the creature as a whole is interfered with by excess as well as by defect. It may be directly interfered with—as for instance by too big an eyelid; and it may be indirectly interfered with, where the organ is large, by needless weight and cost of nutrition. In the second place the question which here concerns us is not what natural selection will do with variations. We are concerned with the previous

Though the counter-opinion of one who is not a naturalist (as Professor Weismann points out) may be of relatively small value, yet I must here again give it, along with a final reason for it. And this reason shall be exhibited, not in a qualitative form, but in a quantitative form. Let us quantify the terms of the hypothesis by weights; and let us take as our test case the rudimentary hind-limbs of the whale. Zoologists are agreed that the whale has been evolved from a mammal which took to aquatic habits, and that its disused hind-limbs have gradually disappeared. When they ceased to be used in swimming, natural selection played a part—probably an important part—in decreasing them; since, being then impediments to movement through the water, they diminished the attainable speed. It may be, too, that for a period after disappearance of the limbs beneath the skin, survival of the fittest had still some effect. But during the latter stages of the process it had no effect; since the rudiments caused no inconvenience and entailed no appreciable cost. Here, therefore, the cause, if Professor Weismann is right, must have been panmixia. Dr. Struthers, Professor of Anatomy at Aberdeen, whose various publications show him to be a high, if not the highest, authority on the anatomy of these great cetaceans, has kindly taken much trouble in furnishing me with the needful data, based upon direct weighing and measuring and estimation of specific gravity. In the Black Whale (*Balænoptera borealis*) there are no rudiments of hind-limbs whatever: rudiments of the pelvic bones

---

question—What variations will arise? An organ varies in all ways; and, unless reason to the contrary is shown, the assumption must be that variations in the direction of increase are as frequent and as great as those in the direction of decrease. Take the case of the tongue. Certainly there are tongues inconveniently large, and probably tongues inconveniently small. What reason have we for assuming that the inconveniently small tongues occur more frequently than the inconveniently large ones? None that I can see. Dr. Romanes has not shown that when natural selection ceases to act on an organ the *minus* variations in each new generation will exceed the *plus* variations. But if they are equal the alleged process of panmixia has no place.

only remain. A sample of the Greenland Right Whale, estimated to weigh 44,800 lbs., had femurs weighing together 3½ ozs.; while a sample of the Razor-back Whale (*Balænoptera musculus*), 50 feet long, and estimated to weigh 56,000 lbs., had rudimentary femurs weighing together one ounce; so that these vanishing remnants of hind-limbs weighed but one-896,000th part of the animal. Now in considering the alleged degeneration by panmixia, we have first to ask why these femurs must be supposed to have varied in the direction of decrease rather than in the direction of increase. During its evolution from the original land-mammal, the whale has grown enormously, implying habitual excess of nutrition. Alike in the embryo and in the growing animal, there must have been a chronic plethora. Why, then, should we suppose these rudiments to have become smaller? Why should they not have enlarged by deposit in them of superfluous materials? But let us grant the unwarranted assumption of predominant *minus* variations. Let us say that the last variation was a reduction of one-half—that in some individuals the joint weight of the femurs was suddenly reduced from two ounces to one ounce—a reduction of one–900,000th of the creature's weight. By inter-crossing with those inheriting the variation, the reduction, or a part of the reduction, was made a trait of the species. Now, in the first place, a necessary implication is that this *minus* variation was maintained in posterity. So far from having reason to suppose this, we have reason to suppose the contrary. As before quoted, Mr. Darwin says that "unless carefully preserved by man," "any particular variation would generally be lost by crossing, reversion, and the accidental destruction of the varying individuals." * And Mr. Galton, in his essay on "Regression towards Mediocrity," † contends that not only do deviations of the whole organism from the mean size tend to thus disappear, but that deviations in its components

* *The Variation of Animals and Plants under Domestication*, vol. ii. p. 292.
† *Journal of the Anthropological Institute* for 1885, p. 253.

do so. Hence the chances are against such *minus* variation being so preserved as to affect the species by panmixia. In the second place, supposing it to be preserved, may we reasonably assume that, by inter-crossing, this decrease, amounting to about a millionth part of the creature's weight, will gradually affect the constitutions of all Razor-back Whales distributed over the Arctic seas and the North Atlantic Ocean, from Greenland to the Equator? Is this a credible conclusion? For three reasons, then, the hypothesis must be rejected.

Thus, the only reasonable interpretation is the inheritance of acquired characters. If the effects of use and disuse, which are known causes of change in each individual, influence succeeding individuals—if functionally-produced modifications of structure are transmissible, as well as modifications of structure otherwise arising—then this reduction of the whale's hind limbs to minute rudiments is accounted for. The cause has been unceasingly operative on all individuals of the species ever since the transformation began.

In one case see all. If this cause has thus operated on the limbs of the whale, it has thus operated in all creatures on all parts having active functions.

At the outset I intimated that I must limit my replies to those arguments of Professor Weismann which are contained in his first article. That those contained in his second might be dealt with no less effectually, did time and space permit, is manifest to me; but about the probability of this the reader must form his own judgment. My replies thus far may be summed up as follows:—

Professor Weismann says he has disproved the conclusion that degeneration of the little toe has resulted from inheritance of acquired characters. But his reasoning fails against an interpretation he overlooks. A profound modification of the hind limbs and their appendages must have taken place during the transition from arboreal habits to terrestrial habits; and dwindling of the little toe is an obvious consequence of disuse, at the same time that enlargement of the great toe is an obvious consequence of increased use.

The entire argument based on the unlike forms and instincts presented by castes of social insects is invalidated by an omission. Until probable conclusions are reached respecting the characters which such insects brought with them into the organized social state, no valid inferences can be drawn respecting characters developed during that state.

A further large error of interpretation is involved in the assumption that the different caste-characters are transmitted to them in the eggs laid by the mother insect. While we have evidence that the unlike structures of the sexes are determined by nutrition of the germ before egg-laying, we have evidence that the unlike structures of classes are caused by unlikenesses of nutrition of the larvæ. That these varieties of forms do not result from varieties of germ-plasms, is demonstrated by the fact that where there are varieties of germ-plasms, as in varieties of the same species of mammal, no deviations in feeding prevent display of their structural results.

For such caste-modifications as those of the Amazon-ants, which are unable to feed themselves, there is a feasible explanation other than Professor Weismann's. The relation of common ants to their domestic animals—aphides and coccids—which yield them food on solicitation, does not differ widely from this relation between these Amazon-ants and their domestic animals—the slave-ants. And the habit of being fed, contracted during the first stages of their parasitic life, when there were perfect males and females, may, during that stage, have become established by inheritance. Meanwhile the opposed interpretation—that this incapacity has resulted from the selection of those ant-communities the queens of which laid eggs that had so varied as to entail this incapacity—implies that a scarcely appreciable economy of nerve-matter advantaged the stirp so greatly as to cause it to spread more than other stirps: an incredible supposition.

As the outcome of these alternative interpretations we saw that the argument respecting the co-adaptation of co-operative parts, which Professor Weismann thinks is furnished to him by the Amazon-ants, disappears. The ancestral ants were conquering ants. These founded the communities; and hence those members of the present communities which are most like them are the Amazon-ants. If so, the co-adaptation of the co-operative parts was effected by inheritance during the solitary and semi-social stages. Even were there no such solution, the opposed solution will be unacceptable. These simultaneous appropriate variations of the co-operative parts in sizes, shapes, and proportions, are supposed to be effected by simultaneous variations in the "determinants" of the germ-plasms; and in the absence of an assigned physical cause, this implies a fortuitous concourse of appropriate variations, which carries us back to a "fortuitous concourse of atoms." This may just as well be extended to the entire organism. The old hypothesis of special creations is more consistent and comprehensible.

To rebut my inference drawn from the distribution of discriminativeness, Professor Weismann uses not an argument but the blank form of an argument. The ability to discriminate one twenty-fourth of an inch by the tongue-tip *may* have been useful to the ape: no conceivable use being even suggested. And then the great body of my argument derived from the distribution of discriminativeness over the skin, which amply suffices, is wholly ignored.

The tacit challenge I gave to name some facts in support of the hypothesis of panmixia—or even a solitary fact—is passed by. It remains a pure speculation having no basis but Professor Weismann's "opinion." When from the abstract statement of it we pass to a concrete test, in the case of the whale, we find that it necessitates an unproved and improbable assumption respecting *plus* and *minus* variations; that it ignores the unceasing tendency to reversion; and that it implies an effect out of all proportion to the cause.

It is curious what entirely opposite conclusions men may draw from the same evidence. Professor Weismann thinks he has shown that the "last bulwark of the Lamarckian principle is untenable." Most readers will hold with me that he is, to use the mildest word, premature in so thinking. Contrariwise my impression is that he has not shown either this bulwark or any other bulwark to be untenable; but rather that while his assault has failed it has furnished opportunity for strengthening sundry of the bulwarks.

PRINTED BY BALLANTYNE, HANSON AND CO
LONDON AND EDINBURGH

DESCRIPTIVE SOCIOLOGY;

OR GROUPS OF

SOCIOLOGICAL FACTS,

CLASSIFIED AND ARRANGED BY

HERBERT SPENCER,

COMPILED AND ABSTRACTED BY

DAVID DUNCAN, M.A. (now Professor of Logic and Director of Studies at Madras); RICHARD SCHEPPIG, Ph.D.; and JAMES COLLIER.

EXTRACT FROM THE PROVISIONAL PREFACE.

Something to introduce the work of which an instalment is annexed, seems needful, in anticipation of the time when completion of a volume will give occasion for a Permanent Preface.

In preparation for *The Principles of Sociology*, requiring as bases of induction large accumulations of data, fitly arranged for comparison, I, some twelve years ago, commenced, by proxy, the collection and organisation of facts presented by societies of different types, past and present; being fortunate enough to secure the services of gentlemen competent to carry on the process in the way I wished. Though this classified compilation of materials was entered upon solely to facilitate my own work; yet, after having brought the mode of classification to a satisfactory form, and after having had some of the Tables filled up, I decided to have the undertaking executed with a view to publication; the facts collected and arranged for easy reference and convenient study of their relations, being so presented, apart from hypothesis, as to aid all students of social science in testing such conclusions as they have drawn and in drawing others.

The Work consists of three large Divisions. Each comprises a set of Tables exhibiting the facts as abstracted and classified, and a mass of quotations and abridged abstracts otherwise classified on which the statements contained in the Tables are based. The condensed statements, arranged after a uniform manner, give, in each Table or succession of Tables, the phenomena of all orders which each society presents—constitute an account of its morphology, its physiology, and (if a society having a known history) its development. On the other hand, the collected Extracts, serving as authorities for the statements in the Tables, are (or, rather will be, when the Work is complete) classified primarily according to the kinds of phenomena to which they refer, and secondarily according to the societies exhibiting these phenomena; so that each kind of phenomenon as it is displayed in all societies, may be separately studied with convenience.

In further explanation I may say that the classified compilations and digests of materials to be thus brought together under the title of *Descriptive Sociology*, are intended to supply the student of Social Science with data, standing towards his conclusions in a relation like that in which accounts of the structures and functions of different types of animals stand to the conclusions of the biologist. Until there had been such systematic descriptions of different kinds of organisms, as made it possible to compare the connexions, and forms, and actions, and modes of origin, of their parts, the Science of Life could make no progress. And in like manner, before there can be reached in Sociology, generalisations having a certainty making them worthy to be called scientific, there must be definite accounts of the institutions and actions of societies of various types, and in various stages of evolution, so arranged as to furnish the means of readily ascertaining what social phenomena are habitually associated.

In Royal Folio, Price 18s.

No. I. ENGLISH.

COMPILED AND ABSTRACTED BY

JAMES COLLIER.

In Royal Folio, Price 16s.

No. II. MEXICANS, CENTRAL AMERICANS, CHIBCHAS, AND PERUVIANS.

COMPILED AND ABSTRACTED BY

RICHARD SCHEPPIG, PH.D.

In Royal Folio, Price 18s.

No. III. LOWEST RACES, NEGRITO RACES, AND MALAYO-POLYNESIAN RACES.

COMPILED AND ABSTRACTED BY

PROF. DUNCAN, M.A., D.Sc.

In Royal Folio, Price 16s.

No. IV. AFRICAN RACES.

COMPILED AND ABSTRACTED BY

PROF. DUNCAN, M.A., D.Sc

In Royal Folio, Price 18s.

No. V. ASIATIC RACES.

COMPILED AND ABSTRACTED BY

PROF. DUNCAN, M.A., D.Sc.

In Royal Folio, Price 18s.

No. VI. AMERICAN RACES.

COMPILED AND ABSTRACTED BY

PROF. DUNCAN, M.A., D.Sc.

In Royal Folio, Price 21s.

No. VII. HEBREWS AND PHŒNICIANS.

COMPILED AND ABSTRACTED BY

RICHARD SCHEPPIG, PH.D.

In Royal Folio, Price 30s.

No. VIII. FRENCH.

COMPILED AND ABSTRACTED BY

JAMES COLLIER.

Unterdeutsch Verfass

11

THE ALL-SUFFICIENCY OF NATURAL SELECTION.

A REPLY TO HERBERT SPENCER.

I.

THE following essay is written as an answer to two articles by Herbert Spencer, one of which, "The Inadequacy of Natural Selection," appeared in the CONTEMPORARY REVIEW in February and March of this year, and is directed chiefly against my views on heredity and natural selection; while the other was published in May, as a "postscript" to the first, and is entitled, "Professor Weismann's Theories." I am never willing to enter into controversy, when the only object is to show others to be in the wrong; but I do so in this instance, as an opportunity is afforded me of expressing opinions on the subject of natural selection that I have long desired to make public, and for the utterance of which I might not otherwise have found occasion so soon.

Any one who has carefully studied the development of the problem of heredity in the course of the last ten years knows that my view of the intransmissibility of acquired characters has not yet received general assent and recognition among scientists. Many still believe that such transmission can be proved; and not a year passes without some "convincing" instances being published. Most of these depend on imperfect comprehension of what is to be understood by an "acquired" character; not a few, however, seem at first sight to be really conclusive against my view.

Among the latter I reckon, for example, the observations which Mr. Buckman, an English geologist, published last year.* It is well-known that the little toe of our foot is more or less deformed: not only small, but curved; and this is commonly ascribed to the boot-pressure to which it is subjected during the greater part of our life;

* S. S. Buckman, "Some Laws of Heredity, and their Application to Man," in *Proceed. Cotteswold Naturalists' Field Club*, vol. x. part iii. p. 258. 1892.

while it is assumed that the injurious effect of the pressure is inherited. This would be transmission of an acquired character. Yet it was possible to reply that perhaps the deformity of the toe arose in the course of each individual life, and was thus always acquired anew—an explanation which would appear to receive support from the circumstance that the little toe of our new-born children lies quite straight. Buckman has now, however, observed in the case of his own children, that the toe becomes curved, even if the children wear no boots, but go barefoot; and this happens as early as six months after birth. He concludes from this, quite rightly, that curvature of the little toe is *inherited*, and he believes that he has thus furnished an illustration of the transmission of acquired characters: he entertains no doubt that the deformity of the toe is due to boot-pressure.

This assumption, however, is erroneous. We have a very exact anatomical and statistical study of the little toe by W. Pfitzner,* from which it appears that *it is undergoing a slow process of degeneration, which cannot be ascribed to boot-pressure*: † it is on the point of changing from a three-jointed to a two-jointed toe. Among forty-seven feet examined at the Strassburg Anatomical Institute, thirteen cases of synostosis of the second and third phalanges of the little toe occurred; and Pfitzner was able to demonstrate the same fusion of the joint in children under seven years of age, and in certain cases even in embryos. His researches were not at all meant to solve the difficulty as to the transmission of acquired characters; he seems, indeed, not even to have known that any such difficulty existed, for he quite ingenuously examines whether the cumulative effects of heredity could have aggregated the very slight atrophy of the toe that might possibly be produced by boot-pressure in individual cases. He negatives this question on the ground that the Japanese and negroes, who go barefoot, exhibit similar fusion of the phalanges. ‡

At my request Professor Wiedersheim was kind enough to investigate the little toe of several Egyptian mummies; and it appeared that among these, too, the fusion of the phalanges could be demonstrated, and not only among adults, but also in the case of children.

So the matter is in much the same position as the degeneration of the tail of the dog and the cat, which likewise has given occasion for misrepresentation as dependent on the transmission of mutilations. Both organs are undergoing a very slowly increasing degeneration, the explanation of which in the case of the little toe offers even less difficulty than in that of the tail of the domestic dog; for physiology has long shown that the little toe, if of use at all, is of quite insignifi-

* W. Pfitzner, "Die kleine Zehe": *Archiv f. Anatomie u. Physiologie*, 1890. P. 12.

† For the reasons why this explanation is inadmissible, see the original treatise. They chiefly turn on the nature of the change, which is such that it could not have been originated by pressure from the side.

‡ The same fact has recently been demonstrated by Martin in the case of certain Patagonians.

cant value in walking; that it is thus superfluous—at least in its full original development, as still seen among the higher apes. But superfluous parts are no longer controlled by natural selection, are not preserved at the height of their development, but slowly sink through Panmixia. The hereditary degeneration of the little toe is thus quite simply explained from my standpoint.

I will not, however, pause to refute other apparent proofs of the transmission of acquired characters; even were I to refute all that have hitherto been advanced, new ones would assuredly constantly be forthcoming; and so, arguing in this way, we should hardly come to a conclusion. Besides, I have ever contended that the acceptance of a principle of explanation is justified, if it can be shown that without it certain facts are inexplicable. I have therefore ever made it my task to show that the assumption of the transmission of acquired characters is not necessary for the explanation of known phenomena; and I have begun to render intelligible, apart from this belief, a large number of facts that have usually hitherto been only explained with its aid—*e.g.*, the degeneration of parts that have become superfluous, the development of instincts, and the existence of artistic talents in man. But I never for a moment doubted that all was not thus achieved, that there were other facts which apparently could not be explained without this assumption; and among these was that one which Herbert Spencer * has now brought to the front again in his essay in this REVIEW, holding it to be a decisive reason for belief in the transmission of acquired characters—namely, *the harmonious variation of the different parts that co-operate to produce one physiological result* [co-adaptation].

It is not for the first time that the distinguished author of the "Principles of Biology" brings forward this difficulty in opposition to my views; seven years ago he published an essay † founded on essentially the same arguments; and I should willingly have replied at that time, had I not been hindered by the prosecution of other studies. Having for many years been troubled by my eyes, I cannot carry on two pieces of work at once.

The following is a summary of Herbert Spencer's argument: If a transmission of acquired characters does not occur, then all enduring variations must rest on natural selection; but again, most, if not all useful variations of any one part must be connected with variations of other parts, if they are to be in any degree effective; and often these co-operative changes are so numerous that it is difficult to understand how all, at one time and independently, should possibly arise through spontaneous variations and natural selection. We cannot believe, on the other hand, that all vary together; that, for instance, the

* Herbert Spencer, "The Inadequacy of Natural Selection": CONTEMPORARY REVIEW for February and March, 1893.

† "The Factors of Organic Evolution": *Kosmos*, 1886, p. 241.

enlargement of the antlers of the stag is always necessarily connected with a thickening of the skull and a strengthening of the neck ligament and the muscles of the neck and back; for we know numerous examples which prove that co-operating parts undergo quite distinct, even opposing, variations. How, if it were otherwise, could the great differences between the fore and hind feet of the kangaroo appear; or how could the powerful nippers of the common lobster arise on the pair of limbs that in the rock lobster bear simple little claws; and so on? One must then, Mr. Spencer thinks, believe that the co-operative parts vary independently of one another. But if this be assumed, then the process of change becomes not only protracted and complicated to an unlimited degree, but simply impossible; for how should all the co-operating parts offer at the same time suitable variations to be preserved by natural selection? Yet the enlargement of the antlers, for instance, requires a simultaneous strengthening of the ligament and the muscles that support the more heavily burdened head; even the processes of the dorsal vertebræ must vary in conformity with the increase; and so must the bones, muscles, ligaments, nerves, and vessels of all these parts, and of the whole anterior extremity. Can these hundreds of individual parts be supposed, independently of one another and simultaneously, to be modified in due proportion, and preserved by natural selection? But if they do not vary *simultaneously* then the variation of individual parts is of no avail; a strengthening of the muscles and ligaments of the neck, without an increase of the antlers avails nothing, and an increase of the antlers unaccompanied by a strengthening of the ligaments, muscles, &c., would be dangerous and highly disadvantageous.

There is thus no apparent alternative but to believe with Mr. Spencer that functional variations are transmitted, and that in this way all co-operative parts remain in harmony; *i.e.*, the variation of *one* part,—as, for instance, the antlers—is always accompanied by an exactly proportionate variation of the others, so far as is beneficial for the general efficiency of the parts. If this be so, belief in the transmission of acquired characters is unavoidable; and Herbert Spencer is so thoroughly convinced of the strength of his argument that he goes the length of saying: "Either there has been inheritance of acquired characters, or there has been no evolution."

I am of a different opinion. Since I expressed the belief ten years ago, that functional variations (acquired characters) could not be transmitted, I have not ceased to test that view, and whenever I have been able to get a more thorough understanding of the facts, I have found it confirmed. But I freely grant that Mr. Spencer's objection is a tempting one; and I should not be surprised if many who read his essay, and are familiar with the enormous difficulties, which, according to his view, stand in the way of an explanation of the facts in question through natural selection, should be carried away by the strength of his skilful representation, and hold the *easier* explanation of the facts—by the inheritance of acquired characters—to be the *correct* one.

I hope to show, however, that it *cannot* be the correct one, and that we must, here, as in the case of the degeneration of disused parts, set aside the apparently simple and almost matter-of-course explanation, and seek another.

What is simpler and more obvious than that organs which are not used degenerate, just because they are inactive? We know that activity invigorates muscles and many other parts, while inactivity renders them weak and thin; for a full explanation, then, we only need to assume that this deterioration is transmitted from generation to generation! Assuredly this idea is simple, but it is wrong. It is plainly contradicted by the fact that parts that are only *passively* functional, that is, such as are useful through their mere presence, as, for instance, the skin and skin-armature of crabs and insects, or the protective colouring of insects, degenerate likewise from the moment they become useless.

If it were possible to show that variations of a complicated structure, whose activities are dependent on many other "co-operating parts," have proceeded without the possibility of the transmission of acquired characters coming into play, then there would be evidence that this last bulwark of the Lamarckian principle is untenable. And there are such cases, as it seems to me.

It fortunately happens that there are animal forms which do not reproduce themselves, but are always propagated anew by parents which are unlike them. These animals, which thus cannot transmit anything, have nevertheless varied in the past, have suffered the loss of parts that were useless, and have increased and altered others; and the metamorphoses have at times been very important, demanding the variation of many parts of the body, inasmuch as many parts must adjust themselves so as to be in harmony with them.

I refer to the neuters of the state-forming insects, especially the ants and termites. Among the latter there are usually two kinds of these, soldiers and workers: among the ants, as a rule, there are only the so-called workers. Every one knows that these "neuters" do not commonly propagate; their organs of reproduction remain small, and in most of the forms that have been fully investigated can be said to be quite rudimentary. But though they do not propagate, or do so only exceptionally, they yet differ from their parents, the males and females, more or less markedly in other parts of the body besides the reproductive organs, and these differences have increased and multiplied in the course of time.

This fact did not escape Charles Darwin, though he did not bear it in mind in dealing with the question which occupies us now. In the "Origin of Species" there is a lengthy discussion of the origin of the neuter ants; and the explanation there given must still be regarded as the only possible one—namely, that they arose through selection of the parents. Darwin's endeavour was to defend the doctrine of evolution and the theory of selection against all possible objections, and to set aside the obvious difficulties; and as such an "apparently insuperable difficulty" he discussed the existence of neuters in the insect states. He accounted for their origin by supposing that a selection of the fruitful females must have taken place, inasmuch as females which produced sterile offspring in addition to fruitful issue were of special value to the state; for the existence of members that were *workers* only was a gain to it and strengthened it, and assured it a superiority over other colonies that had no workers. So in course of time the states with workers conquered those with none, and in the end caused them to disappear. In the same way all the variations among the workers arose, to make them more fit to be of service to the state.

It may be difficult to think out such a slow and indirect selection; but we must nevertheless hold this explanation to be correct, as it is the only possible one, unless, indeed, an inner developmental force is assumed to originate the metamorphosis of organisms, as by Nägeli and others. I long ago, however, produced ample evidence* that such a "phyletic developmental force" is contradicted by innumerable facts. It would only be reconcilable with the very exact adaptation of all organisms to their conditions of life, by the assumption at the same time of a "pre-established harmony" between the life-conditions and the nature of the metamorphosis, so that every tiniest change in the former would be quite exactly limited as to time and place, and would correspond to a hair's breadth with the similarly limited variations in the organism. Leibnitz, as is well known, conceived body and soul to be related in this way, and compared them to two clocks so constructed as always to go exactly alike, though independent of one another.

Such a hypothesis would not suit the author of the "Principles of Biology"; and as he, moreover, recognises the efficiency of natural selection, he will require no other explanation of the occurrence of the neuters than the Darwinian, unless he would seek to contest the facts—to which I shall return. But, as soon as he has recognised this explanation to be the right one, he will have granted, at the same time, that not only degeneration of parts, but even the harmonious and efficacious metamorphosis of many co-operative parts can proceed without any concurrence of the transmission of acquired characters.

* "Studien zur Descendenztheorie," Leipzig, 1876, pp. 295 and 322: Eng. trans., "Studies in the Theory of Descent," part iii., London, 1882, pp. 664 and 706.

I proceed now to the proof. The ants are animals whose life and doings, as well as their organism, have been most minutely investigated. A long list of excellent observers have thought them worthy of prolonged research; and many of these, as, for instance, P. Huber, A. Forel, and the Jesuit Father Wasmann, have devoted their lives, giving all their time and all their energy, to them. We have, then, such a large store of admirable information concerning the ants that our theoretical conclusions regarding them can be founded on a firm foundation; and for this reason I leave the termites, as to which our information is much less certain and exact, altogether out of account.

That the *ant-workers* have arisen through phyletic metamorphosis of fruitful females may well be taken for granted, without explicit proof. What other origin could they have had? And this is the view taken by all recent investigators from Forel to Wasmann. To this day there are some species (*e g.*, *Leptothorax acervorum*) in which the workers closely resemble the females, and in the same species, forms intermediate between the females and workers have frequently been found. Wasmann * established no fewer than six different categories of such transition forms. As to the *nature of the modifications* which distinguish the workers and females, they are partly *retrogressive*, partly *progressive* or dependent on a fuller development of certain parts.

Retrogression in the ovaries and receptaculum seminis is found among the workers of all the species of ant that have been examined. We are indebted to the researches of a Swedish naturalist, Adlerz, for exact information on this subject; and from his work it appears that the receptaculum has completely disappeared in all the species studied by him, and that the ovaries have degenerated in various degrees: in one species twelve egg-tubes persist in each ovary, in another only one to five, in a third only three, in others only one or two; in *Tapinoma* and almost all the *Myrmicida* there is only one, while in *Tetramorium* there are none at all.

Retrogression is also found in the *eyes of the workers* of many species. The three ocelli are often wanting altogether; and the number of facets in the compound eyes, and, as a consequence, the quality of the eyes, is more or less reduced, compared with that of the males and females of the same species. Forel has given us the results of many exact observations on these relations; for instance: the male of *Formica pratensis* has about 1200 facets in each eye, the female of the same species has only 830, but the worker has only some 600; again, the male of the common turf-ant, *Solenopsis fugax*, has more than 400 facets, the female about 200, while the worker has only 6–9.

* E. Wasmann, "Ueber die verschiednen Zwischenformen von Weibchen und Arbeitern bei Ameisen"; *Stettiner Entomolog. Zeitung*, 1890, p. 300.

That the males should have the most highly developed eyes cannot surprise us, as we know that this is very often the case among insects; there are even species of Ephemerids (*Potamanthus*) in which the male, in addition to the common compound eyes, has others quite distinct, large and turban-shaped, on the top of its head, so that it has a very peculiar appearance. The truth is, it is the males that seek out the females, and therefore their better sight is of advantage to them during the nuptial flight high up in the air. The females, too, use their eyes during the flight; and it is only the workers, which always live and labour on the ground, and largely, even, in dark places, that are restricted to a limited use of their organs of vision.

But perhaps some will doubt whether there is here an actual degeneration in the workers and not simply a higher development of the compound eyes of the males and females. I hold it to be quite possible that in certain cases the compound eyes of the males and females have increased since the institution of a worker type; but that reduction has, at the same time, taken place in the workers' eyes is proved not only by the disappearance of the ocelli in many species, but by cases like that of *Solenopsis fugax;* for the females of no living species in which a nuptial flight occurs have eyes composed of so few as only 6–9 facets, and accordingly the ancestors of the ants must have had large compound eyes, like all predatory hymenoptera that have not become state-formers.

Again there has been retrogression in the wings of the workers, and so complete that there is no appearance of them in the perfect insect. But in this case, too, it can be proved that the ancestral forms possessed wings; for Dewitz has demonstrated the imaginal discs of the wings in the larva, though they develop no further in the pupa.

Besides the wings, the two segments of the thorax on which the wings are situated, as well as the muscles of the thorax which move the wings, have degenerated in the workers. The latter point has been directly established by Adlerz in the case of *Camponotus* and *Formica*, but could also be inferred from the marked reduction of the two posterior thoracic segments. These segments are, at the same time, much more simply constructed than in the males and females; the ridges which bound the small shield-shaped areas of the mesothorax, the so-called scutellum and pro-scutellum, are wanting altogether, and so is the post-scutellum, while the two little side-pieces, which lie under the usual position of insertion of the posterior wings, are fused. The changes in the thorax are thus just such as would necessarily arise through transmission of the deteriorating effects of disuse, if there were any such inheritance. *But the workers are sterile, and can transmit nothing at all.*

Likewise rudimentary among the workers are all the instincts which are concerned with reproduction.

I have elsewhere attempted to show that all these degenerations in the sterile members of the state-forming insects can only be explained by Panmixia, as where there are no heirs there can be no transmission of the effects of disuse. Moreover, a degeneration of the wings cannot be accounted for by transmission of the consequences of disuse, even if the workers had progeny; for the wings of insects are passive organs, whose perfection in no way depends on their being employed; they are complete before they are used, and are rather injured by wear than strengthened by use. I long ago* pointed out other similar cases (skin-armature of hermit-crabs, &c.), and can only explain Mr. Spencer's ignoring such cogent instances by supposing that, as a philosopher, he is unacquainted with the facts by personal observation, and that therefore they appear less weighty to him than to a naturalist; for I would not for a moment suppose that he purposely evades the difficulties which face his opinion, as is the manner of popular orators and advocates—and alas! even of some scientists.

It is the ants, too, that suggest another interesting case, which proves that degeneration of an organ does not depend on the transmission of functional atrophy, but that there may be degeneration of an organ even when it continues to function. The reduction in the number of facets in the eyes of the workers would not be referable to the transmission of functional atrophy, even if the workers reproduced themselves, for their eyes are not much less exposed to the light than in earlier days when they were fertile females. We have not to do with animals that live in absolute darkness, but alternately in the light and in the dark, just like the females, which are similarly situated except as regards the nuptial flight. The eyes of the workers are thus in fact not out of use; they are exposed to the light nearly as much as those of the females, and can therefore certainly not fail through lack of function. But they degenerate *because, and in so far as, they are superfluous for the full performance of the tasks of a worker*; so, in this way again, we are led to Panmixia.

The second group of variations which have appeared among the workers are progressive developments of certain parts; and, above all, the great increase in the brain has to be named. This is connected with the higher intelligence and manifold instincts of the workers, whose functions, as is well known, are of varied nature and partly of a kind that could only exist through the formation of states and the existence of a working-class. But even externally the workers are not infrequently distinguished by peculiarities which are closely connected with their activity, and so cannot have been transmitted from the sexual forms, and in course of time lost by these. Among these characteristics are, for instance, the long thorns which the workers of some species (*e.g.*, *Atta*) have on the head and back.

In *Atta*, too, the workers are distinguished from the females by yet

* "Aufsätze über Vererbung," u. s. w., p. 571, English trans., vol. ii. p. 20.

more evident marks. In certain species two forms of workers occur, one of which, because they undertake the defence of the colony, are usually called "soldiers," and these are often very different from the other workers, and still more from the females. Thus, in *Pheidole megacephala* the head of the soldiers is much larger, and is equipped with far more powerful jaws, and the size of the head allows the muscles which move the jaws to be of quite unusual dimensions, as Lubbock, who has studied the life of this South-European species,* points out.

In the Mid-European species, *Colobopsis truncata*, Emery has also discovered two worker-forms, and the "soldiers" in this case are so distinct from the common workers that they had previously been held to be a different species (*C. fuscipes*) when they were found in the nest of *Colobopsis truncata*. Here again the soldiers have a large and thick head, which they make use of in a very peculiar way. It is so large that it just fills up one of the many little approaches to the nest, and so the soldiers keep guard, each of them holding possession of a doorway.

It can hardly be gainsaid that we have here variations in which, in lesser degree, processes must be involved similar to those Herbert Spencer has justly assumed in the case where the head of a stag (*e.g.*, the Irish elk) is loaded with ever larger and heavier antlers; that is to say, *many parts must have varied simultaneously and in harmony with one another*. If the jaws became stronger and larger, they could only continue to be useful provided the muscles that move them became stronger, and if the chitinous capsule of the head, to which they are attached, became thicker. The head must thus have become larger, and the cuticle thicker at the same time; likewise the nerves which supply the masticatory muscles must have become richer in fibres, so as to be able to supply all of the much more numerous muscle-fibres; and in a corresponding degree the appropriate motor-centres in the brain must have undergone an increase of their elements, and so on. Yet with all this we are not done; for as in the stag the heavier horns required a strengthening of the ligaments, bones, and muscles of at least the neck and anterior extremities, so the larger and heavier head of the ants that have been metamorphosed into soldiers could no longer have been supported and moved by the thorax and limbs, if there had not been an increase in the firmness of the skeleton and in the joint-membranes, muscles, and nerves of these parts.

None of these changes can rest on the transmission of functional variations, as the workers do not at all, or only exceptionally, reproduce; they can thus only have arisen by a selection of the parent ants dependent on the fact that those parents which produced

* Sir John Lubbock, "Ants, Bees and Wasps."

the best workers had always the best prospect of the persistence of their colony. No other explanation is conceivable; *and it is just because no other explanation is conceivable, that it is necessary for us to accept the principle of natural selection.* It alone can explain the adaptations of organisms without assuming the help of a principle of design. Mr. Spencer complains bitterly that in my essays the words, "it is easy to imagine" are frequently used; and thinks many of my arguments are based on things "easy to imagine." Perhaps the expression is blameworthy, in so far as it permits conclusions to be drawn from inadequate evidence; but I am glad to be able to say that I have really not used it, at least not in the way complained of by Mr. Spencer. My opponent has overlooked the fact that the English edition of my Essays is not the original, but a translation. The expression "it is easy to imagine" is not mine at all, but is a somewhat too free translation of various phrases in the original German. The passage specially referred to by Mr. Spencer reads thus in the German edition (p. 92): "so könnte man immerhin daran denken dass . . . ;" which is not at all so matter-of-course as "it is easy to imagine" implies; and a translation faithful to the meaning, if not very elegant English, would read somewhat as follows: "one could perhaps even think to explain this by assuming . . . ." In another passage ("Aufsatz," VIII. p. 525) the "it is easy to imagine" rests on the words: "es ist also an und für sich durchaus nicht unzulässig"; in a third ("Aufsatz," IV. p. 235) there is: "allein es wäre ja ganz wohl denkbar"; and out of the eight places in which the expression occurs* in the English edition, there are only two in which it stands likewise in the German, and my severe critic will assuredly have nothing to say against its use in these. On page 156 of the first English edition, these words occur: "In all these cases it is easy to imagine the operation of natural selection in producing such alterations in the duration of life . . . ."; and on page 430: "we can easily imagine how it happened, when we learn that tailless cats are especially prized in Japan. . . . ." I think a naturalist may well endeavour to conceive in concrete form facts which he has inferred; there is even a certain degree of confirmation of what has been merely inferred, when it is possible to form a conception of it that goes into details. The truth of the inference does not, indeed, depend on our being able to do this, but follows from the convincing strength of the deduction,—naturalist and philosopher are at one as to this, *in theory*, at least.

It seems to me, though, that *in practice* my opponent is almost

* One of my friends has taken the trouble to look through the English edition of my Essays for the expression "it is easy to imagine." He did not find it in Essays I., V., VI., VII., IX., X., XI., and XII.; it occurs twice in II., once in III.; in IV. the word "imagine" appears three times in a somewhat different connection; and "easy to imagine" is also twice in VIII.

more disposed than I to justify assumptions by the ease with which they can be imagined. He sets aside the possibility of explaining complicated harmonious metamorphoses of the body (co-adaptations) by natural selection, because such varied and involved contemporaneous processes of selection cannot be imagined; but, on the other hand, he assumes the extraordinary height of the giraffe's body to be due to natural selection, because here the process appears easy to imagine. The truth is, he is compelled to this assumption in the second case, because the Lamarckian principle of the transmission of functional variations fails him; for as he says, a lengthening of the leg and neck through stretching up for high twigs cannot be suggested.

I must say that, in respect of warrant to assume the process of natural selection, it does not seem to matter much whether we can easily, or with difficulty, or only with great difficulty, imagine it; and for this reason, that I do not believe that we are in any case able to conceive in detail the actual morphological metamorphoses concerned. I, too, refer the length of the neck and forelimbs of the giraffe to processes of selection; but I contend that we can only conceive these quite generally and very indefinitely. There are no data for a fuller conception; we know neither how great must be the changes which are able to decide for life or extinction; nor do we know how often variations occur to be accumulated by selection; nor even how often, at what intervals of time, they result in selection. We know, indeed, nothing at all but the chief foundation of the process; and therefore any one who does not comprehend the logical necessity of the theory, or will not recognise it, can easily set aside the individual instances as untenable. Herbert Spencer seems not to know that Nägeli * in a book that attracted much attention among scientists ten years ago, analysed this very case of the giraffe, and attempted to show that processes of selection could by no means explain the height of the giraffe.

My opponent thinks further that the extraordinary delicacy of the tip of the tongue cannot be explained by processes of selection, and that I would certainly not contend that any person ever succumbed in the struggle for existence because he had a less sensitive tongue-tip than others. Such a result, apparently, seems to Mr. Spencer difficult to imagine. And it is so, because we see only very imperfectly into the life-struggle of animals, and still more because we so readily forget that in such highly developed organs as the tongue of man we have to do with the final result of an endless perfecting process, which has been going on through thousands and thousands of species, a process which, again, we are quite incapable of representing to

* "Mechanisch-physiologische Theorie der Abstammungslehre." München u. Leipzig, 1884.

ourselves at all adequately. Our imagination does not grasp such immense successions of time and such long-protracted lines of development; we speak of them without rightly knowing what we say, pretty much as when we talk of billions or trillions; we must reduce the immense multitude to a unity to be able to work with it, for the multiplicity exceeds our experience too far; and that is easily forgotten. Moreover, in many animals, and, indeed, in those that are most nearly related to man, the apes—as Romanes * has already very rightly pointed out in reply to Spencer—the tongue is an organ of touch, and has not only to function in the mouth, moving the food during chewing, but serves at the same time as a hand, and is used for the examination of external substances. Why then should there not be a decided advantage in the struggle for existence to those individuals in which it is more delicately constructed than in the others of the same species. The life of animals necessarily depends on the acuteness of their sense-organs.

But, truly, in this case there is refuge for the followers of Lamarck in the transmission of acquired characters, provided it can be assumed that the touch papillæ of the tip of the tongue have ever increased in number through much use. There are examples enough, however, in which it is possible to exclude this hypothetical factor, and I should like to adduce one of these, which has long seemed to me to be a good proof of how little depends, in the assumption of processes of selection, on whether we can readily or with difficulty conceive them.

Very many insects, and particularly the bees and wasps, have on the lower end of the tibia of the anterior leg a slightly movable spur-shaped process, and opposite this, on the metatarsus, there is a small, nearly crescent-shaped notch, which is beset with a comb of minute teeth; and this "strigil" serves for the cleansing of the antennæ, the part that is to be cleansed being drawn between the spur and the strigil, as if between the two blades of a pair of scissors. F. Dahl,† in particular, has investigated and figured this interesting and very delicate arrangement, as it is found in many insects; and Canestrini and Berlese ‡ had written on it somewhat earlier.

The strigil, then, forms an abrupt and very striking interruption of the surface of the leg, and in one of the small bees, *Nomada*, has quite the appearance as if some one had struck out with a punch a crescent-shaped piece from the limb, so sudden and regular is the notch. It looks as if the insect, through ever and again drawing its antenna between spur and tarsus, had gradually produced this crescentic notch. But that would be to assume transmission of

* Herbert Spencer on "Natural Selection" in CONTEMPORARY REVIEW, No. 823, April 1893, p. 499.

† F. Dahl, "Beiträge zur Kenntniss des Baues u. der Functionen der Insectenbeine." Berlin, 1884.

‡ Canestrini and Berlese, "La streggia degli Imenotheri." Padua, 1880.

acquired characters, which in this case is excluded by the fact that the function of the cuticular skeleton is purely passive. Insects have their legs fully formed when they leave the pupa, and, as they do not later undergo exuviation, there can be no suggestion of a functional variation of the chitinous skeleton, which is no longer a living part of the insect, but a derivative from the underlying layers of living cells. Even if the cleansing of the antennæ acts like a file, only dead substance will be removed, much as when we file down the finger-nails; and assuredly even the most stiff-necked believer in the transmission of acquired characters would hesitate to maintain that such a defect could be transmitted.

As this explanation is not possible, then, there remains only that of natural selection. It is again "easy to imagine" that it must be of advantage for the insect to be able to free such important sense-organs as the antennæ from dust and dirt; but, as soon as the attempt is made to think out the process in detail, we recognise that here, too, we know nothing thoroughly, and that it would be uncommonly easy for any one who wished to assign the processes of natural selection altogether to the realm of phantasy to emphasise this view; for *it is really very difficult to imagine this process of natural selection in its details;* and to this day it is impossible to demonstrate it in any one point. As a sudden origin of the strigil is excluded, we should have to assume that the notch began, in some members of the species, by the appearance of a small depression of the strongly convex surface of the metatarsus at the site of the future strigil, and that, in the struggle for existence, these individuals had thereby an advantage over others. How easy, however, would it be for an opponent to doubt this superiority. He might, perhaps, be ready to believe that an insect which has no means of cleansing its antennæ would be at a disadvantage compared with another which has such means, but he would say that it was absurd to believe that so trifling an improvement in the cleansing apparatus as is represented by a slight depression of the tarsus could be decisive as to which should succumb and which survive.

Dozens of similar objections have been raised against the occurrence of natural selection, and not by ignorant and superficial thinkers only, but by very learned and thoughtful men of science: I need only instance Nägeli once more. We cannot compel such an antagonist to take our view, at least not as regards any single instance, for we cannot prove that which he doubts: we are unable to show by direct evidence that such a small advantage can turn the balance in favour of life or death; and much less that it must do so in many cases, and in generation after generation, till finally the variety with a shallow depression is the dominant one. All that we can do is to show the utility of the perfected arrangement, by removing, as Forel did, the anterior tibia with the strigil from such an insect and establishing that very soon the antennæ become dirty, and the insect is no longer able to clean itself.

But though the process of natural selection, which we must insist on, *began* with the formation of a slight depression opposite the spur, it was very far from ending with that. How does it come about, our opponent will say, that the gradual deepening of the depression proceeds so regularly that at last a quite deep, crescent-shaped hole has arisen? Is it possible that only such variations were advantageous and decisive between life and death as exhibited perfectly regular progress from the initial depression to the final, well-cut semi-globular hollow? And how can it be believed that somewhat less regular deepenings, which must have occurred along with the regular ones, always, again and again, brought about the death of the insects in which they appeared? Lastly, the depression of the strigil is also beset with microscopic teeth: did every one of these, if they arose by chance variations, give the verdict between life and death, before becoming a fixed possession of the species?

To the first objection we could perhaps answer that the processes of natural selection are very protracted; and therefore the notch, which was perhaps irregular at first, may have become ever more regular in the course of untold generations, always because the strigil served its purpose so much better the more perfectly it fitted the form of the antenna that had to be cleansed. We might remark that the strigil of different living species is developed in very different degrees, and that, from its common occurrence among the insects, we may infer that it has been undergoing continual, slow improvement since the earliest days of insect life on the earth. But this, too, may make no impression on my adversary, who calmly continues to assert that such a tiny improvement could not give the decision for life or death. And the same is repeated in connection with the last objection, when, perhaps, the answer has been given that the teeth which clothe the strigil have arisen, not individually, but all at once, at first as a slight roughness of the chitinous surface, then as ever more prominently projecting and more regularly formed points.

Just as in this instance, so is it in every individual case of natural selection. We cannot demonstrate any of them, and there is no use attempting to make them seem unanswerable by having recourse to the co-adaptation which Mr. Spencer brings forward. Moreover, I believe there are hardly any metamorphoses which do not involve the harmonious variation of *several* parts, in the production of a useful structure. It is so in the case of the strigil, for the spur of the tibia which is opposite the excavation in the metatarsus forms the other limb of the scissors through which the antennæ are drawn during the cleansing process; and it, too, by its free movement and by its peculiar sinuations, is exactly suited to its function. So selection must have affected it, also; for here again, *variation because of function is excluded*, as the spur is only *passive* in its function. It is true the results of artificial selection are in favour of the occurrence of natural selection, but as Herbert Spencer justly observes, the two processes, though they may be analogous, are certainly not identical. The struggle for existence plays the part of breeder in the case of natural selection; and how this factor works we are unable to determine in any single case. Who would say of any little variation in the form of any existing species that it is sufficient to give its possessor the victory in the struggle for existence, and so may become the starting-point of an advantageous metamorphosis of the part? Even in the simplest of cases that is impossible; no one, for instance, could decide how much the colour of a green insect must vary, so as to originate a process of selection dependent, perhaps, on adaptation to a new and somewhat differently coloured fodder-plant. We cannot estimate what Romanes has recently very well called the "selection-value" * of variations, which Lloyd Morgan had previously spoken of as the "elimination value"; we can only say generally with Darwin that selection works by the accumulation of very slight variations, *and conclude from this that these "slight variations" must possess selection-value.* To determine accurately the degree of this selection-value in individual cases, is, however, as yet impossible.

So when any one asks with Herbert Spencer: Do you believe that a little *plus* of perceptiveness in the tip of the tongue has ever been decisive as to who shall perish and who survive? one may reply in the affirmative, and another in the negative, with equal right; for one finds it easy, the other difficult, to imagine; and neither of these judgments is convincing.

The question might also be put: Do you believe that when the eggs of a bird whose surroundings are grey acquire a faint grey tint the victory is thereby secured over the original white? To that many nowadays would assuredly answer Yes; but some would as certainly say No; and in my opinion both would be wrong, for how should we know the selection-value of these variations?

But let us go on to ask: Do you believe that a variety of robber-fly with *one* facet more in the compound eye than the other members of the species have, will from that derive so great advantage that it will leave behind it more descendants than the others; or must there

* In physiological variations it is somewhat different, though even here numerical values cannot be given. If, for instance, some plants of a southern species withstand the frosts of winter, while most succumb to them, we have an indication of selection-value; but we know nothing of the structural changes, except their effects and their utility for the northward-pressing colony of the species. That the species is, because of these changes, able to spread northwards is not implied, but depends on many other factors.

be *two* facets more; or would selection-value only be attained by a difference of *ten?* Who is able to say that he can affirm anything on the subject? And yet, apart from natural selection we have no explanation of the wonderfully exact adaptation of the compound eyes of all insects to their life-conditions.

Thus we could ask questions for ever without getting a definite answer. But let me put one more, which will lead us back to our consideration of the ants: Do you believe that the fine bristles on the broad metatarsus of the honey-bee have arisen because slight variations of the female bees, leading up to this result, have been of so great value as to secure the survival of the hive over others? The answer of many will be that this is not only *difficult* to imagine, but that it is quite incredible, seeing that the workers have themselves no advantage from the change, and do not live longer or better on account of it; and that it only enables them to carry a little more pollen at a time to the hive, and to feed the bee larvæ a little more abundantly or quickly, which could not possibly be decisive for the extinction or survival of this family of bees in competition with other families. If one realises that the workers are sterile, and that, accordingly, not they themselves, but their parents, the sexual bees, must have been the subjects of selection dependent on whether they brought forth better or worse workers, then it becomes quite unthinkable that such tiny variations as the slight broadening of the metatarsus, or a denser coating of bristles on it, could ever have given the verdict for or against the continuance of the parent-bees.

I am, of course, not of this opinion, but believe that here, as in the case of the ants, every little improvement in the workers proceeds from the variation of a determinant of the germ-plasm that was contained in the germ-cells of the parents. For fuller explanation I would venture to trust to the theory set forth in my recently published book.* According to it the dimorphism or polymorphism of a species is represented in the germ-plasm by the doubling or multiplying of certain determinants, while it depends on certain conditions, which are for the most part unknown to us, which of the representative determinants or groups of determinants become active, and which remain passive. By "determinants" I mean units of the germ-plasm that are the primary constituents of definite cells or groups of cells of the body. When, now, corresponding parts appear in two forms in any species; when, for instance, the scales of a certain part of the wing of a species of butterfly are brown in the female, but blue in the male, this is provided for in the germ-plasm, according to my view, by the determinants of the wing-scales occurring doubled, one set representing the primary constituents of brown scales, the other of blue. Both cannot become active in the same individual—*i.e.*, cannot

* "The Germ-Plasm: A Theory of Heredity." London: 1893.

lead to the formation of scales, but while one set remains inactive the other is destined for activity.

So when, instead of dimorphism, there is polymorphism, when, for instance, the females of a species are similarly distinguished among themselves, and occur in two forms, this results, according to my idea, from the double determinants becoming triple determinants. If there were workers among the butterflies, and if these showed red colour on the part of the wing that is blue in the male and brown in the female, there would always be three representative determinants present at a definite part of the extremely elaborate and highly complicated germ-plasm; but only one of these would become active during the development of the egg or sperm-cell concerned, and would produce the patch of brown or blue or red scales on the wing.

According to this theoretical representation, every part of the body of the bee or ant that is differently formed in the males, females, and workers is represented in the germ-plasm by three corresponding determinants, but on the development of an egg, never more than one of these attains to value—*i.e.*, gives rise to the part of the body that is represented—and the others remain inactive.

Thus, then, the metamorphosis of the body-parts of the workers of ants and bees will have to be considered in connection with the fact that the males and females whose germ-plasm contains favourable variations of the determinants of the workers have a better prospect for the maintenance of their successors than others which show less favourable variations of such determinants. The process of selection is the same as if the matter at issue were the attainment of favourable adaptations in the body of the sexual forms; for in both cases it is, as I once before said, not really the body that is selected, but the germ-plasm from which the body develops. The difference is this: in the one case the survival in the struggle for existence depends on characters and variations of the body of the individual; in the other, only on the character of a certain kind of descendant—the worker. If the ant-state were composed of individuals connected together like a colony of polypes or *Siphonophoræ*, a process of selection by which only the workers were changed would be within easier reach of our imagination, as these would then, in a manner, be only *organs*, just like the snaring-threads, the swimming-bells, and the gastric tubes of the *Siphonophoræ*. As these do not reproduce, and accordingly can only vary by selection of the egg or germ-plasm from which the whole colony is formed, so in the case of the ant-colony, or rather state, the barren individuals or organs are metamorphosed only by selection of the germ-plasm from which the whole state proceeds. In respect of selection the whole state behaves as a single animal; the state is selected, not the single individuals; and the various forms behave exactly like the parts of one individual in the course of ordinary selection.

From this point of view a circumstance that must otherwise appear unmeaning becomes intelligible, namely, *the limitation of the fertile females of a hive to a single one*, as is the case among the honey-bees. Were many females of a hive engaged at one time in the production of eggs, the natural selection that depends on the quality of the brood of workers brought forth would be far more difficult and much slower, inasmuch as the prosperity of the hive would depend on many differently constituted workers, and so, in some measure, only the resultant of the produce of all these females would be selected: a queen would by no means be doomed to extinction because she produced a bad race of workers, for her hive would at the same time be provided with a brood of workers by other queens, and if the majority of these produced better workers, the hive would perhaps hold their own against others in the struggle for existence for a long time, till at last the worser worker-brood distinctly preponderated in the hive. Obviously the workers must be more rapidly improved when all in a hive are the progeny of one queen—*i.e.*, if they are all alike or almost alike. The hive would survive in the struggle for existence if this one queen produced better workers, if, consequently, the brood was more quickly and better cared for, if more provision were made for the winter, and so a lower mortality prevailed in the hive. I could almost suppose that the remarkable reduction of the fertile females to a few (termites) or only one (bees) has taken place because the gradual improvement of the sexless by natural selection can thus to some extent proceed more easily and more rapidly; or rather, the hives with few queens had an advantage, because they could improve themselves relatively more quickly. It seems to me that the selection of workers is "*easier to imagine*" in these circumstances, though truly only in principle and not in detail. As soon as an attempt is made to think out in detail the process of selection by which, perhaps, the little bristles or the small baskets of the worker-bees have arisen, it is seen that all and every one of the data are wanting. Moreover, in my opinion we cannot hope that we shall ever possess them, either in these cases or in any yet simpler process of natural selection. Not only would it be necessary to form an estimate of the smallest variations, so as to know whether and how often among 1000, 100,000, or millions of individuals there is a variation which gives verdict over life and death: but much more that we can never determine is required; for instance, the number of individuals of a species living at one time, the degree of their mingling with one another in their own domain, and the percentage occurrence of the variation in question. All which, I am convinced, cannot be ascertained; and so we shall never be able to establish by observation the progress of natural selection.

What is it then that nevertheless makes us believe in this progress as actual, and leads us to ascribe such extraordinary importance to it? Nothing but the power of logic; we must assume natural selection to be the principle of explanation of the metamorphoses, because all other apparent principles of explanation fail us, and it is inconceivable that there could be yet another capable of explaining the adaptations of organisms, *without assuming the help of a principle of design.* In other words, *it is the only conceivable natural explanation of organisms regarded as adaptations to conditions.*

Certainly one could not know *a priori* whether other factors did not take an important part in bringing about the metamorphosis of species, and till twenty-five years ago, I myself entertained the opinion that besides primary variations and their accumulation and arrangement by natural selection, the inherited results of use and disuse played a not unimportant part. It looks quite as if it were so, as Mr. Spencer very plainly shows by his illustrations of the harmonious metamorphosis of many and diverse co-operating parts proceeding parallel with use. But does it not seem to be true that unused parts degenerate directly because of disuse? And that is not so, as I think I formerly proved, and have now confirmed with facts. If the eyes of the workers of many species of ant degenerate, although the animals do not propagate, and though their eyes are hardly less exposed to the light than those of the sexual forms by which they are produced, the change *cannot possibly* depend on transmission of the effects of disuse. And if harmonious metamorphosis of the head and all its co-operating parts and those of the thorax has occurred among some of the sterile ant-workers, this must also have taken place without any co-operation of the hypothetical transmission of functional variations. Against this conclusion there is no resource: once the facts are established, there is no escape left.

Are then the facts disputable? That is the question that remains to be considered.

The supporters of the Lamarckian principle can urge that the sterility of the ant-workers is not absolute; that it has been proved that now and then they produce eggs, from which, though of course they remain unfertilised, males proceed; and that this is sufficient for the transmission of the characters of the mother-worker. The reply to which might be the following: It is true that in many species the workers occasionally produce eggs (Forel, Lubbock, Wasmann). This is especially the case when they are in confinement and under artificial conditions, particularly when the temperature is high; but it occurs, so far as we know, only exceptionally. But even if a small percentage of the males were to arise from such eggs, there could never be an equal distribution of the characters of the workers through the entire colony as a result; for the few males that are produced by the workers have to contend with the far greater number of males produced by queens. If it were the case that all the males of the colony proceeded from the eggs of workers, and if the queens had only female offspring, the objection would indeed be justified; and then the ants could no longer serve as an illustration of the occurrence of metamorphosis of species in circumstances that precluded the possibility of the transmission of functional variations; but so far as our knowledge goes, the case is otherwise. I know, it is true, of no observation that directly demonstrates that the queens produce both males and females, as has long been established for the bees; but the opposite view—that the queens produce no males—is much further from being proved. If we recollect that even the bee-workers in certain circumstances produce eggs, from which, as among the ants, only males arise; and further reflect that the ovary has degenerated in very different degrees in the various species of ant, in *Solenopsis fugax*, for instance, all the egg-tubes having disappeared, so that *sterility is complete*; we shall be compelled to hold it to be extremely improbable that in any of the species the duty of producing males has devolved on the workers exclusively. Rather we shall have to take the view that in the course of the phylogenetic development of the workers, first there was diminution in fruitfulness, accompanied by disappearance of the *receptaculum seminis*—which implies that only unfertilised eggs could be produced; then this limited reproduction became rarer and rarer, while the number of egg-tubes continually declined; and at last in *Solenopsis fugax*, with the disappearance of the last egg-tube the fall-off in productiveness was complete. This agrees with the opinions of our best specialists; and Forel, in his great work on the ants of Switzerland, affirmed that *infertility was one of the essential characteristics of workers*, and that it was only because of this infertility that they had become more capable of performing the many tasks that now fall to their lot than the fertile females, which are burdened with many eggs.

If any hope is left to the Lamarckians that this mighty mass of evidence supplied by the ants can be got rid of, this is the point on which that hope must depend; and so I would meet in anticipation yet another attack. Forel has frequently observed that *old* ant-colonies contained only males; and the attempt might be made to infer from this that there had been only workers in the colony, and that these had produced the males. But the fact is capable of a much more natural explanation, if one remembers that the same is true of the bees: there are hives in which neither young workers nor queens are found, but only males (drones); and we know that these males are the offspring of a so-called "drone-breeding" queen—*i.e.*, of an old queen whose supply of sperms has been exhausted, and which accordingly is no longer able to fertilise the eggs which she lays. In the case of the ants exactly the same will occur; and we know from Lubbock's observations that queen ants may live to be fifteen years of age, which gives time enough to exhaust the sperms in their receptacle.

It might, perhaps, be said that the workers had only lost their fertility late in the course of phylogeny, and after they had undergone the other metamorphoses. But this assumption is untenable, as both the bodily structure and the activities of the workers are closely connected with their unproductivenes. Forel holds strongly that the production of sterile individuals was the first stage in the development of the workers. According to his view, the working power of a state was first increased by the decline of fertility in a large number of the females, while, as a consequence, there was a constant improvement in strength, intelligence, and activity, and a gradual disappearance of parts that had become useless: of wings, because there was no longer a nuptial flight; and of ocelli and a part of the compound eye for the same reason.

It would be possible, moreover, to doubt the sufficiency of this argument, and yet believe sterility to have appeared after the other characters. In this case, at least *one* question would remain for the Lamarckians to answer: *how did the production of sterile forms come to be established as a hereditary arrangement?* Certainly not by transmission of functional variations; for this variation, sterility essentially excludes inheritance.

Moreover, there is another way to show that after the appearance of sterile workers new variations were still possible, and even such as involved the simultaneous change of many parts in harmony with one another. This is implied in the occurrence of certain *species with two kinds of workers*, one of which must have sprung from the other by gradual metamorphosis. I have spoken above of the soldiers of *Pheidole megacephala* and *Colobopsis truncata*, whose immense heads and jaws could only have arisen from the corresponding parts of the other workers by harmonious metamorphosis of many distinct parts.

But some will doubt whether the soldiers really have sprung from the other workers by gradual metamorphosis, and will perhaps say that they might as well have been directly derived from fertile females, and only have lost their fertility when the other changes were completed. Against this idea, however, we have the fact that many stages in the development of double worker-forms exist at the present day, and so enable us to infer the history of their origin. Some species exhibit slight differences in the size of the workers; in others the differences are markedly greater though the larger workers are still connected with the smaller by many of intermediate size; then there are species in which these connecting-links are wanting; and these lead to others in which, accompanying the increase in size, there are other changes: in form and in instincts. The soldiers have thus not arisen independently of and simultaneously with the other workers, but have been formed in accordance with the principle of division of labour by further differentiation of already existing workers, that is to say, *at a time when the present sharp distinctions between females and workers had long been established, and the regular reproduction of the latter had long ceased.*

If any one still doubts that all the various metamorphoses of females to workers have come about independently of direct transmission, and so not according to the Lamarckian principle, I would refer him to a study of certain instincts of the ants, and their consequences as regards the organisation of the workers. By the custom, or rather instinct, to make and keep slaves most remarkable changes have appeared in the slave-holders; and these can only be explained by natural selection as the slave-making impulse must have arisen long after the formation of workers. Most species of ants make no slaves; but some species occasionally do, and at other times do not, as, for instance, the much discussed *Formica sanguinea*, which has been very carefully observed in many lands. In this species the workers often go forth to hunt; they break in upon a colony of another species (*e.g.*, *F. pratensis*), and carry off the pupæ to their own nest. This instinct, however, is not yet a firm possession of the species, for there are colonies in which no slaves are found; so it may be assumed that slavery has been introduced in relatively recent times, and in accord with that view is the fact that in *Formica sanguinea* there have been no changes in structure and habit like those that appear in *Polyergus rufescens*, all the colonies of which contain slaves, and among which, accordingly, the slaving instinct has become a fixed specific character. Between these two phylogenetic stages—that of *Formica sanguinea* and that of *Polyergus rufescens*—lies the origin of the remarkable changes to which I have referred as resulting from the slaving-instinct in *Polyergus*, namely, *the metamorphosis of the jaws from useful tools to deadly weapons and very admirable transport apparatus, and the degeneration of the ordinary instincts of the workers. All these must indisputably have come about without any co-operation of transmission of functional variations.*

The jaws of *Polyergus rufescens* have lost the so-called chewing-edge. Ants do not really chew in the literal sense, but they lick; frequently, indeed, they use their jaws to tear their food to pieces; but the chief purposes for which the jaws are employed are connected with all manner of household work; they serve for the transport of eggs, larvæ and pupæ, hither and thither; for dragging building materials along; for the formation of passages, cells, and spaces in the nest; and for mining in wood or in the ground, &c. In *Polyergus* the workers have forgotten all such household instincts; they no longer trouble themselves about their young, but leave them entirely to the care of slaves; they bring in neither food nor building materials, as the slaves sufficiently supply these; they do nothing but fight, and steal the pupæ of other species, and carry these away to their nests. Accordingly their jaws are metamorphosed to sabre-shaped, pointed and powerful nippers, which serve as a deadly weapon that the ant is wont to employ in piercing the heads of its enemies, and at the same time are remarkably well adapted for the transport of plundered pupæ, as the jaw-nippers can embrace the body of the pupa without injuring it. This exact adaptation of the jaws for the stealing of pupæ can only be explained by selection of the germ-plasm of the parents of the workers; and the same can be said of the strongly developed fighting-instinct, of the great courage displayed, and of the instinct that leads these ants to steal the pupæ of others, and carry them away to their nests. Here, then, we have *positive selection.*

On the other hand we have *negative selection* or Panmixia in the decline of the ordinary instincts of the workers: those that are concerned with care of the young, nest-building, the storing of food, while *most uncommon and most instructive of all is the degeneration of the instinct to search for food.*

Herbert Spencer in his essay likewise attacks Panmixia, and attempts to show that I mean by this name the selection of the less injurious, and that nothing can be explained by this. He considers my example of the blind cave animals (*e.g.*, *Proteus*), and gives it as his opinion that it is impossible that the principle of the economy of growth can here have given the verdict for life or death, inasmuch as the difference in the size of the eyes of the individual varieties must have been much too trifling. So far I agree with him thoroughly. But Panmixia is, according to my representation of it, something quite different from the survival of the least unsuitable; it is the deterioration of organs from the height of their development *through the non-disappearance of such individuals as possess them in less perfect form.* In my opinion all organs are maintained at the height of their development only through uninterrupted selection, and decline incessantly, though at the same time excessively slowly, as soon as they cease to be of value for the maintenance of the species. That is what I have called Panmixia, as Professor Romanes recently very properly pointed out in the reply to Mr. Spencer to which I have already referred. The principle of economy was only introduced by me as a possible secondary cause of degeneration. The words actually used in the case of the *Proteus* are these:

"*Possibly* accessory is the fact that smaller and degenerated eyes may now"—after the retrogression of the organ has begun—"even be advantageous, inasmuch as other organs which have become more important for the creature, such as the tactile and olfactory organs, may be all the more strongly developed. *But even apart from this,* the eye will necessarily decline from the height of its development, slowly, very slowly indeed, especially at the beginning of the process—but *surely* from the moment it is no longer maintained at this height by natural selection. Similarly *all* cases of degeneration, whether of organs or species, may be explained in a simple manner." *

How far-reaching the principle of economy may be in certain cases of degeneration cannot easily be determined; but that my former opinion was correct, according to which *Panmixia alone* suffices to bring about the complete disappearance of characters, is proved, among other things, by the above-mentioned degeneration in the warlike amazon-ants (*Polyergus rufescens*) of the instinct to search for food. Not only the males and females, but the workers of these ants, have altogether forgotten how to recognise their food. Forel, Lubbock, and Wasmann have all satisfied themselves that Huber's old statements on this subject are correct, and I myself have repeated his and Forel's experiments with the same results. The animals starve in confinement, unless some of their slaves are present to feed them; they do not recognise a honey-drop as something that would appease their hunger, and when Wasmann placed a dead pupa between their jaws, they did not begin to eat, but at most licked it in a tentative way and withdrew. But as soon as a slave—for instance, a worker of *Formica pratensis*—is put beside them, they come to it and beg for food; and the slave runs to the honey, and having filled its crop, proceeds to feed its lords.

So it is not the feeding instinct that is wanting here, as has often been said, but rather the capacity to seek and recognise the food. To be exact: the instinct to take food is *not aroused by the sight of food, but by the sight of the slave.* It appears as if these amazons had through the constant presence of slaves that were ever ready to feed them, gradually lost the habit of seeking food, and at the same time had come to regard the slaves as food-providers. It seems an excellent example of the direct effects of disuse and the transmission of functional degeneration—if only these amazons were not sterile!

The one possible explanation is that of Panmixia. As the amazons, because of the constant presence of slaves, never suffered want, the perfection of the instinct to seek food ceased to be an element in deciding which should survive and which should perish. Individuals with badly developed feeding instinct were, *cæteris paribus*, quite as good as others; and colonies in which such individuals occurred did not decline sooner on that account. Thus this instinct must slowly have fallen from its original perfection, and finally, though assuredly after an immensely long series of generations, quite disappeared. I fully grant that this is very "difficult to imagine"; but it must have occurred, as all other explanations are excluded by the infertility of the amazons.

* "Aufsätze,' p. 568, 569.

We are unacquainted with the particulars of the material foundation of instincts, and do not know in what cells or fibres of the brain this instinct is situated, but be that as it may, there is no doubt that the saving of material substance consequent on the decline of the instinct is so trifling in amount that it is very improbable that the principle of economy has, in this case, played even an accessory part. So we have here an instance of *complete disappearance of a character, for the explanation of which we are compelled to turn to the principle of Panmixia.*

This is not the place to enter into details as to this principle of explanation, which is simply an inference from a general acceptance of the principle of selection as an efficient factor in all adaptations. Once it is admitted that the adaptations of parts are always due to selection, it follows from the occurrence of variation, itself the chief factor in selection, that they are also maintained by selection. For though a useful character must become all the more constant, the longer the period through which it has been confirmed by constantly repeated selection, yet observation proves that no character, however old it is, ever attains to perfect constancy; but always slight variations occur. Therefore, as soon as selection ceases to affect a character, it must slowly begin to decline from the stage of development already reached.

This consequence of selection was not propounded by me for the first time; but as we have recently learned, was urged ten years ago by Romanes;* and if this acute investigator did not succeed in bringing his correct inference into favour with scientists, it was because he did not give up the transmission of acquired characters, which he still adheres to; thinking, like Spencer, that, having regard to the harmonious metamorphosis of co-operating parts (co-adaptation), it is not possible to dispense with the principle of the transmission of functional variations; and so he continues to regard me as an "ultra-Darwinian." But Romanes in 1874 made the cessation of selection only of subsidiary importance, supposing it to support other factors, especially "economy of growth" and "disuse," in bringing about the degeneration of disused parts. He says: "The cessation of selection should therefore be regarded as a reducing cause, which co-operates with other reducing causes in all cases, and which is of special importance as an accelerating agent, when the influence of the latter becomes feeble." But if, as he thinks, disuse is directly effective through the transmission of functional atrophy, and economy of growth also co-operates in the degeneration of organs, then it would be impossible to demonstrate the influence of the cessation of selection, inasmuch as its effects would necessarily always be mixed

* *Nature*, vol. ix.: "Natural Selection and Dysteleology," in the number for 12th March, 1874; in the number for 9th April, 1874, a second article: "Rudimentary Organs"; and in the number for 2nd July, 1874, a third: "Disuse as a Reducing Cause in Species."

up with those of the other factors. If only Romanes had considered the workers of the state-building insects, he would have recognised that the factor whose influence he rightly inferred, can *unaided* bring about degeneration, that it is thus the *chief* factor. At the same time, however, this would necessarily have upset his conviction that there is transmission of functional variations; and he would not have concluded his article with the words: "However, as before remarked, the question thus raised is of no practical importance, since whether or not disuse is the principle cause of atrophy in species, there is no doubt that atrophy accompanies disuse."

Thus it happened that a conception that was fully justified could not find favour, and all but fell into oblivion. Romanes thought that disuse only partially explained degeneration, and that "cessation of selection" subsequently set in. So the difference in the reduction of the wings of ducks and geese, in spite of equal disuse, would be intelligible: the variations in the species having been correspondingly different. This quite agrees with my opinion, inasmuch as Panmixia must, in truth, depend, as regards the time of its activity, on the variability of the species concerned; and it is this that in such cases as that of duck and goose indicates that *disuse is not the true cause* of organs becoming rudimentary. Romanes was very near the truth, but did not reach it; he continues thus:

"I deem it in the last degree improbable that disuse should not have assisted in reducing the unused organs of our domestic animals, and the effect of this remark is to show that *the cessation of selection is not able to accomplish so much reduction as I antecedently expected.* On the other hand, it seems to me no less improbable that the cessation of selection should not have here operated to some extent; but in what degree the observable effects are to be attributed to this cause, and in what degree to disuse, I shall not pretend to suggest."

I myself was led to the discovery of the principle of Panmixia through serious doubt as to transmission of acquired characters. If there was no such transmission, then there must be another cause of the disappearance of useless parts to be discovered; and so I was led to Panmixia. When I was compelled to deny both the transmission of functional atrophy and the transmission of the effects of the principle of economy in the individual ontogeny, the new principle was at once demonstrated as active: there remained for me only the *one* explanation of organs becoming rudimentary, that of selection, either *negative* selection alone (Panmixia), or with the aid of *positive* selection, which prefers, and gives the victory to, the less injurious. Of course I can only speak of the principle of economy in this latter sense, which, moreover, was understood by Spencer, and not in the sense of a transmission of effects of the struggle of parts in the course of ontogeny. I would also specially emphasise the fact that after full consideration of the relations among the ants, I am more disposed, even, than ten years ago, to regard the principle of economy as a very unimportant factor in reduction, and one which, in most instances, probably takes no part at all.

Assuming, now, that we have proved that the transmission of functional variations has had no share in producing the harmonious variations of many co-operating parts in the case of the ant-workers, we must consider with what right we may look upon natural selection as the active factor.

The answer is very simple: *with the same right as we have for believing in its activity anywhere else in nature.* As already indicated, we accept it, not because we are able to demonstrate the process in detail, not even because we can with more or less ease imagine it, but simply *because we must, because it is the only possible explanation* that we can conceive. For there are only two possible *a priori* explanations of adaptations for the naturalist—namely, the transmission of functional adaptations and natural selection; but as the first of these can be excluded, only the second remains. It has often been said that proof of the actual intervention of natural selection in the development of organisms has not yet been produced; we can readily imagine its occurrence, but there is no cogent reason for the belief. This is indeed true; but I think that proof, based on the relations among the ants, can be produced.

First, even without the help of this exceptionally favourable instance, it is possible to lead proof of probability. That natural selection is really an active factor, and that variation, heredity, and the struggle for existence—*i.e.*, the decimation of progeny—actually produce the adaptations of organisms to their environment is not only rendered highly probable by the fact that all organisation is revealed as adaptation as soon as it is rightly understood, and that the three named factors are proved to be efficient, but the probability is greatly increased by our *knowledge of the artificial selection that is practised by man.* In this analogous process there are two factors, variation and heredity, just as in the assumed natural selection, and only the third factor is different.

The high theoretical value of artificial selection seems to me to consist in the assurance it gives us of the ascending and cumulative effects of the first two factors in natural selection. If we had had to do without this, it would have been difficult to prove natural selection; for our knowledge of the fundamental processes of variation and heredity is much too limited to enable us to anticipate the consequence on the offspring of the combination of similar or dissimilar parental characters. Artificial selection, however, has provided us with a rich store of experience, and *we may now confidently found on the fact that improvement and general variation in definite directions can come about through selection of parents that are specially suited for the breeder's purpose.*

This, however, is the foundation of the process of natural selection.

We know that changes in definite directions can be produced by selection, and it only remains to consider the third factor of the process, the one that regulates the selection; and this factor, the struggle for existence, happens to be one that leaves no doubt as to its general activity.

That there are variations which must lead to victory in the struggle for existence is beyond doubt, though we cannot recognise them as such in advance; the survival of the fittest is certain, but we do not know in individual cases what is fit, nor yet how often in every generation it survives, and must survive, if it is to gain the victory. We cannot then, as a rule, produce evidence that a particular adaptation has arisen by natural selection. But if, as in the case of the ants, the other possible explanation, that of the transmission of functional variation, can be excluded, *we have a demonstration, at least for the particular instance, of the actual occurrence of natural selection.*

And now we are justified in further concluding that if in this one definite but many-sided instance the struggle for existence acts as natural selection assumes it to act, that is, like the breeder who in artificial selection chooses what suits him, then *even the small variations which occur in all parts of the body may possess selection value;* and if that is so in this case, there is no reason why they should not in countless other analogous cases have the same significance; in other words, *natural selection effects all manner of adaptations.*

We are thus able to prove by exclusion the reality of natural selection, and once that is done, the general objections which are based on our inability to demonstrate selection-value in individual cases, must collapse, as being of no weight. Therefore I shall not attempt here to give an exhaustive explanation of harmonious variation. It does not matter whether I am able to do so or not, or whether I could do it well or ill; once it is established that natural selection is the only principle which has to be considered, it necessarily follows that the facts can be correctly explained by natural selection. The explanation may be difficult, and through lack of data it may be impossible to put it beyond doubt; but the fact is not thereby contradicted, just as the view of modern physiologists that there is no peculiar vital force is not negatived, though to this day we cannot explain even a single vital process by purely physical forces. I believe, however, that an approximate and general explanation of harmonious variation (co-adaptation) is now possible, and I shall elsewhere attempt to give such an exposition; but, whatever its defects may be, no evidence can be drawn from them in favour of the transmission of functional variations, which seems to me to be definitely discredited now that it has been ousted from its last lurking-place—the harmonious variation of co-operating parts. When it is remembered that direct proof of such transmission is wanting, and that accordingly the justification for its acceptance has rested only on its being apparently indispensable for the explanation of certain facts, it must be admitted that now that it has been shown that these facts occur where transmission of functional variation is excluded, there is no longer any sufficient reason for assuming this principle of explanation in any other case. If the workers of an ant-state can change into "soldiers," and can vary a large number of co-operating parts harmoniously without any help from the supposed transmission of functional variations, then there is no reason why we should deny the same capability to the stag or the giraffe. It would be illogical to assume a new and unproved force in these cases, after the analogous metamorphoses in the ants have been shown to occur without any such force. To that Mr. Spencer must agree, for he says: "A recognised principle of reasoning —the law of parsimony—forbids the assumption of more causes than are needful for explanation of phenomena" (p. 750).

Accordingly I hold it to be demonstrated that all hereditary adaptation rests on natural selection, and that natural selection is the one great principle that enables organisms to conform, to a certain high degree, to their varying conditions, by constructing new adaptations out of old ones. It is not merely an accessory principle, which only comes into operation when the assumed transmission of functional variations fails; but it is the chief principle in the variation of organisms, and compared to it, the primary variation which is due to the direct action of external influences on the germ-plasm, is of very secondary importance. For, as I previously said, the organism is composed of adaptations, some of which are of recent date, some are older, some very old; but the influence of primary variations on the physiognomy of species has been slight and of subordinate importance. Therefore I hold the discovery of natural selection to be one of the most fundamental ever made in the field of biology, and one that is alone sufficient to immortalise the names of Charles Darwin and Alfred Wallace. When my opponents set me down as an ultra-Darwinist, who takes a one-sided and exaggerated view of the principle discovered by the great naturalist, perhaps that may make an impression on some of the timid souls who always act on the supposition that the *juste-milieu* is proper; but it seems to me that it is never possible to say *a priori* how far-reaching a principle of explanation is: it must be tried first; and to have made such a trial has been my offence or my merit. Only very gradually have I learned the full scope of the principle of selection; and certainly I have been led beyond Darwin's conclusions. Progress in science usually involves a struggle against deep-rooted prejudices: such was the belief in the transmission of acquired characters; and it is only now that it has fortunately been overcome that the full significance of natural selection can be discerned. Now, for the first time, consummation of the principle is possible; and so my work has not been to exaggerate, but to complete.

AUGUST WEISMANN.

THE ALL-SUFFICIENCY OF NATURAL SELECTION.

II.

IN a second essay or "postscript," Herbert Spencer attacks some other of my "fundamental theories," the wide acceptance of which surprises him even more than the acceptance of the intransmissibility of acquired characters. These are my views on the distinction in the Metazoa between somatic and reproductive cells and on the immortality of the latter and of unicellular organisms I will consider these objections, too; though I should have wished an opponent who had made himself more familiar with the opinions he criticises than Mr. Spencer has done. His assault is not always directed against the main point in my views; and above all, he has but a partial knowledge of the evidence for them. I regret this, especially because it compels me to repeat to some extent what will already be known to the reader; and also because, as far as science is concerned, such a contest almost seems to me to be a useless waste of energy on the part of both assailant and defender.

Mr. Spencer refers almost exclusively to the first two of my essays; once he quotes the fifth; but he appears to be ignorant of the later ones, and, in particular, the last in the book, the twelfth, which summarises my argument, and gives my conclusions on the very points discussed by Mr. Spencer. As is explained in the preface, the essays were written at intervals during a space of ten years, and published separately; but were subsequently collected, and issued *unchanged* in book form. So they represent, to some extent, the different stages of a continuous research; and the critic who confines his attention to the oldest essays, which belong to the years 1881 and 1883, is contesting only the first and naturally the least satisfactory evidence for my views. My opponent would probably have had fewer objections to state, if he had read the later essays.

Even the form of the criticism would have disposed me to refrain from answering it, had not Herbert Spencer been the author; for it contains more of personalities than in my opinion is proper. The expression, "it is easy to imagine," which, as I have shown, has been quite unwarrantably put into my mouth, is again and again brought up against me, as if this phrase, which is, perhaps, an inexpedient one, justified an inference that my work had been loose.

But let me come to the subject-matter. Mr. Spencer's scientific objections are directed in the first place against my view that the metazoan body is composed of cells of two sorts, somatic and reproductive, which have been differentiated on the principle of a physiological division of labour, for the preservation of the species—the somatic undertaking the providing of sustenance, in the widest sense of the term; and the reproductive cells being concerned with propagation. He begins by designating as fallacious the interpretation that recognises a division of labour in the relations existing between the cells. Division of labour, according to Mr. Spencer, implies an *exchange of services*, but here there is no exchange. In my opinion the expression means that the functions that were formerly performed by every individual of a community are now distributed among the various members; and in this sense the differentiation of a cell-colony, formerly composed of members that were all alike, into somatic and reproductive cells is unquestionably brought about according to the principle of the division of labour, altogether irrespective of whether the somatic cells have any benefit from the reproductive cells. The benefit accrues to the whole colony, or in the case of the distinction in the metazoan body, to the species; and in this sense the expression has been understood by biologists for the last forty years, ever since Rudolph Leuckart taught that the *Siphonophoræ* were to be regarded as colonies of "persons" differentiated "on the principle of the division of labour." Assuredly the expression was borrowed from the relations subsisting in human society, where it can be said to include an exchange of services; but when it is applied to the organism, this part of the conception is given up in favour of the idea of differentiation of parts for the higher general efficiency of the whole. It is a mistake to suppose that there is always an exchange of services, or that "the essential nature of this division of labour" involves exchange. Mr. Spencer asks: "Where is the exchange of services between somatic cells and reproductive cells?" And answers: "There is none." Quite true; the reproductive cells, so far as we know, render no service to the somatic cells; and therefore, as it seems to Mr. Spencer, a cell-colony which consists only of these two elements cannot be differentiated according to the principle of the division of labour. But does not Mr. Spencer himself approve of "students of biology" recognising a "division of labour" in the differentiation of the cell-mass of an organism, by the separation of the cells into those of the skin, of "digestion, respiration, circulation, excretion, &c."? And why has he omitted the reproductive cells, which equally belong to the organism, but to have added which would have been to have contradicted with his own words the idea that exchange of services is of the essence of division of labour? Or to take one of the oldest illustrations of the division of labour: what services do the male or female "persons" of a colony of *Siphonophoræ* render to the "snaring-persons" or the "swimming-bell persons," or the polypes of the colony? Where is the exchange of services? "There is none." So, at least as used by biologists, division of labour does not essentially involve exchange of services; but it implies the distribution of the functions of the community among the different members, and the consequent better development of these functions for the higher efficiency of the community. The distribution of labour is the means employed by "Nature" to bring about the increased efficiency of organisms; without differentiation according to the principle of distribution of labour there would be no higher organisms.

But let us pass from this dispute as to words to consider weightier matters. My opponent thinks I am wrong in believing that the primary division of labour is that between somatic and reproductive cells; and bases his conclusion on my own statement that the differentiation is not always absolute, and that it is only late in the ontogeny of vertebrates that the reproductive cells appear, while among hydroids they may be formed only in later generations. He calls these facts a "crack," even a "chasm," in my theory; and regards them as so destructive of my view that he compares me to the Frenchman who set aside facts that contradicted his opinions with the words, "*Tant pis pour les faits.*"

I must say that I am somewhat amazed at the extraordinary readiness with which Mr. Spencer disposes of the views of others. Is it possible that the author of the "Principles of Biology" does not know that thousandfold derangements, both as regards time and place, occur in the course of development; that, indeed, there is hardly any ontogeny in which derangements do not play their part? If he did not know that, he would have learned it by reading my fourth essay, where it is considered at length in connection with the very subject in question, the genesis of germ-cells. (English edition, p. 205.)

Are we to look for primary conditions in the group of animals that was the last of all to appear, the vertebrates; or among the hydroids, whose mode of reproduction is by alternation of generations, which is likewise a secondary and late-acquired form? Does not the art of discovering the phylogenetic connection of species largely consist in finding out these innumerable derangements in the ontogeny, and tracing the primary relations? How then does the late appearance of the germ-cells in these two groups, and many others besides, prove that the *primary* differentiation was not that of somatic and reproductive cells?

Of course the late differentiation of the germ-cells in the vertebrates and other animals is no evidence that originally they were differentiated at the beginning of the ontogeny; but proof of this is given in my fourth essay (p. 243 Germ. edit.; Eng. trans. vol. i. p. 205), inasmuch as it is shown that to this day in certain lower organisms this condition of the first differentiation of a multicellular form has been maintained; and to make this clearer I have given illustrations of the Algæ *Pandorina* and *Volvox*. In the first of these, division of labour has not yet appeared, and all the cells of the colony attend to both feeding and reproduction. In the nearly related *Volvox*, on the other hand, the cells are divided into somatic cells, for feeding, movement, &c., and reproductive cells. Thus we have preserved to the present day the two consecutive stages in the phyletic development, that are required by the theory. But truly these facts are not evidence to him who is ignorant of them; and I confess that Herbert Spencer's criticism reminds me a little of the man who said: "*I don't know your reasons but I condemn them.*"

Mr. Spencer ignores not only the greater part of my essays, but also the arguments contained in Essay II., which he has read. Immediately after the sentence (p. 74, Eng. trans.) which he quotes, reference is made to my earlier researches on the origin of the reproductive cells among the *Hydromedusæ*, in which it is shown that extensive derangement in the time of their appearance actually occurs. In the fourth essay the same was urged with greater detail, as well as the convincing value of the facts for the proof of the continuity of the germ-plasm. But Mr. Spencer seems to know nothing of the essay on this hypothesis.

The next attack is directed against the immortality ascribed by me to unicellular organisms and germ-cells, in contrast to the mortality of metazoan forms. First it is alleged that I have overlooked a universal law of evolution, which implies the necessity of death. "The changes of every aggregate, no matter of what kind, inevitably end in a state of equilibrium. Suns and planets die, as well as organisms. The process of integration, which constitutes the fundamental trait of all evolution, continues until it has brought about a state which negatives further alterations, molar or molecular." Perhaps I shall be credited when I say that I knew this; but I do not think that it has anything to do with the difference that there is between unicellular and multicellular organisms, in regard to death and continued existence, which alone is discussed in my biological treatises. Moreover I see that at the end of the first essay—which Mr. Spencer has read

—I was careful enough to seek to preclude such a misinterpretation as Mr. Spencer's (Germ. edit., p. 40; Eng. ed., p. 34); for I expressly say: "I have repeatedly spoken of immortality, first of the unicellular organism, and secondly of the reproductive cell. By this word I have merely intended to imply a duration of time which appears to be endless to our human faculties."

But now as to the real question involved: According to my view the protozoa and germ-cells are immortal in the sense just explained—*i.e.*, as my opponent rightly observes, they can divide again and again, so long as the necessary external conditions are favourable. Mr. Spencer disputes the correctness of this, first, on the ground that for many unicellar organisms conjugation is apparently necessary, a process which, as is well known, my opponents regard as "rejuvenescence." My critic thinks—

> "If the immortality of a series is shown if its members divide and subdivide perpetually, then the opposite of immortality is shown when, instead of division, there is union. Each series ends, and there is initiated a new series, differing more or less from both. Thus the assertion that the reproductive cells are immortal can be defended only by changing the conception of immortality otherwise implied."

Mr. Spencer did not need to remind me that a mingling of two individuals is involved in conjugation and fertilisation, as that is precisely *my* view. I hold that the two processes have no other signification, and that is why I applied the name Amphimixis to them. But does that prove that they involve a rejuvenescence? I have frequently disputed this view, and if Mr. Spencer would read my twelfth essay, he would find my reasons for doing so. I should willingly repeat them here, but they require to be treated at length, and the space I can venture to take up here would not suffice. It seems to me that the capacity for unlimited reproduction—*i.e.*, for immortality in the biological sense of the term—is affected as little by the act of amphimixis as by any other act, as, for instance, that of taking food. The latter, too, is necessary for the continuance of the process of division, and in the case of many unicellular organisms must precede division. Though we cannot say that amphimixis is never a necessary condition of immortality, we do know that for the reproductive cells it is not always necessary. Mr. Spencer himself fully explains how the aphides, when in favourable circumstances, can multiply indefinitely by parthenogenesis; but even if amphimixis were an indispensable condition of immortality, *this immortality would still exist: the cells that have conjugated are not dead, but still live and can go on propagating.* My critic seems to be conscious of the weakness of his sophism, for he makes two other efforts to explain away the fact of unlimited fission among the Infusoria. First he doubts the fact, for he asks: "What observer has watched for forty years to see whether the fissiparous multiplication of Protozoa dces not cease? What observer has watched for one year, or one month, or one week?" By reading the essay on amphimixis he might have learned that, as a matter of fact, a French naturalist, Maupas, had with amazing assiduity followed for months the reproduction of the Infusoria. But even if this had not been done, we know that many of our species of Infusoria were in existence in the time of Ehrenberg and O. F. Müller; and this proves, unless the absurd supposition of the spontaneous generation of such highly differentiated forms is assumed, that they have multiplied by constant division through nearly a century. And there are foraminifera extant that existed as early as the tertiary period, and so their fissions have been continued through entire geological periods.

The second attempt to contradict immortality depends on the statement that the two infusoria that coalesce in conjugation *lose their individuality*, and a new individual arises as a result. This is true so far as in fact there is a coalescence of two individuals, as I have shown (Essay XII.); but how does it negative my contention that there is no natural death among the Protozoa? Is conjugation the same as death? Does not the same conjugation or amphimixis occur in the fertilisation of the metazoa; and is this their natural death? If not, then the Metazoa have such a natural death over and above this, and by it they are distinguished from the Protozoa: *Q.e.d.*—for that is all that I have contended for. I have called attention to the fact that here there is an essential difference between Protozoa and Metazoa; that among the Metazoa the differentiation of body-cells and germ-cells appears; and that the "body" is *alone* subject to natural death. Such, too, is the truth; and no sophisms on the part of Mr. Spencer will do away with it. What does he mean by setting forth that in a healthy woman the body-cells continue to multiply by division for long after the germ-cells have died out? When did I say that germ-cells could not die? On the contrary, I have tried to make abundantly clear to my earlier opponents the difference between accidental and natural death, as, for instance, in Essay III. in reply to Götte. Death of such egg-cells as are not fertilised must be regarded as of the same nature as accidental death, or as the death of a wolf from starvation: the conditions of further life are not present.

Mr. Spencer, however, takes a totally different view of the matter; for he denies the mortality of the body, or rather not of the body as a whole, but he asserts that the body-cells are capable of unlimited division. While I refer natural death and the natural endurance of life to a definite adjustment of the power of reproduction of the somatic cells, Mr. Spencer takes the view that their death is brought about by external conditions, and that consequently, in favourable circumstances, they are quite as capable as the reproductive cells of multiplying indefinitely. He takes a great deal of trouble to set forth instances in which species have propagated for an indefinite period by budding, as is well known in the case of numerous plants. Had he read through my essays, or even my recent book on the "Germ-Plasm," he would have spared himself such a tilt against a windmill; for I have explicitly recognised that many somatic cells have the capacity to reproduce indefinitely—namely, such as lead to germ-cells or bud-cells—cells of the "germinal tracks"—and also those cells which give rise to new "persons" by budding. In the first essay, to which Mr. Spencer has referred, there is no mention of this, because at the time it was written it was necessary above everything to set forth, well-defined and clear, the new discovery—I mean the contrast between beings *without* and those *with* a natural death. So I considered only the simpler cases, and tried to explain why the somatic cells have lost the power of indefinite multiplication, without going on to ask whether, among the higher Metazoa, where the germ-cells have undergone re-arrangement, or among colonial forms (*Stöcke*), there do not occur somatic cells which possess this power.

Several years ago, De Vries, in opposition to my view, urged that among plants the difference between somatic-cells and germ-cells was not so great as among the Metazoa, and this I freely granted to him, and added that the same might be said of many colonial Metazoa. In both these instances budding occurs, and implies the presence of cells which have retained the capacity for unlimited multiplication. According to my view, cells from which budding has to proceed must contain the elements that are necessary for the building up of a new individual—*i.e.*, germ-plasm—or, in the cases where several cells co-operate to form a bud, a definite combination of determinants. Those cells that contain germ-plasm in an unalterable condition (*in gebundenem Zustand*) I have expressly called somatic cells, as well as those that represent "germ-tracks"—that is, those that are formed in the course of development from an egg, and are destined to become germ-cells. These cells likewise contain germ-plasm in an inactive condition; and so it is chiefly such somatic cells as have inactive germ-plasm that have retained, or perhaps it would be better to say, have re-acquired, the capacity for indefinite multiplication. I have often urged that these cells do not by any means require to be young cells, but that, on the contrary, they may be histologically differentiated, as, for instance, in the case of the epidermal cells of the leaf of Begonia, from which new plants spring. So there are "immortal" somatic cells, even according to my view [*Cf.* "Germ-Plasm," pp. 186–197]; and in my recent book Mr. Spencer might have found an entire chapter devoted to budding, and, among other things, an attempt to discover the reasons why such cells occur in great numbers among the plants.

There is, however, a difference of opinion between Mr. Spencer and myself as regards the *causes* which condition the mortality of most of the somatic cells of the Metazoa that do not exhibit budding. Mr. Spencer regards external causes as responsible; I look to internal causes. My opponent enumerates nine different factors which co-operate in aiding or restraining cell-multiplication; and which, according to his representation, are sufficient to account for the observed differences in the duration of cell-division. There is, first, the "vital capital" given by the parents; then there is the character of the food; the grade of "visceral development"; the expenditure of energy necessary for the procuring of food; the cost of maintaining the bodily heat; and finally the relations of the mass of the body to the surface, which are of significance from various points of view. It is quite true that all of these factors exercise an influence on the multiplication of cells; but when Mr. Spencer declares that before other causes for the limitation of cell-multiplication are assumed, there must be proof of the inadequacy of those adduced by him, it seems to me that his reasoning is fallacious. It would only have been justified, if an *unknown* force had been assumed to explain the phenomena, as when Mr. Spencer assumes a transmission of acquired characters to explain "co-adaptation." But here the matter is very different: I assume, in explanation of the varying duration of the life of cells, not an unknown force, but a factor that Mr. Spencer has forgotten to adduce, and which is yet the most important of all—namely, the very constitution of living cells. Or is it possible that my critic would deny that the character of the living substance of the cell exercises an influence on its capacity for multiplication? Do all cells multiply equally vigorously and equally long when they are subject to the same external influences? Is not the constitution of the cell the first and weightiest of all the conditions? It can hardly be disputed that this must be added as the tenth cause to the others stated by Mr. Spencer; and, in my opinion, it is the chief one. *The function of the cell depends, first of all, on its constitution; and all else is of secondary importance.* In my twelfth essay it is shown at length that both male and female germ-cells of a nematode multiply quite regularly by a definite number of divisions, and then become incapable of dividing farther. First there are a few divisions of the primary germ-cells; then there is a long interruption of the process of multiplication, and the primary germ-cells grow, and become mother-cells. At this stage another period of multiplication ensues, for each cell rapidly divides twice in succession, and then the capacity for further division ceases, as well in the ripe sperm-cells as in the egg-cells. Which of Mr. Spencer's nine causes can get credit for this regular rhythm? The character of the nourishment, perhaps? But this remains constant throughout. The ovary floats in blood, and while the first-formed germ-cells have already attained to ripeness, others are only giving rise to the formation of mother-cells, and so on. Or is the proportion of the mass of the cell to its surface responsible? But though the ripe egg-cell cannot of itself multiply, yet, as soon as the minute sperm-cell has reached it, it commences to divide more and more, and in a quite different and new sense, which can have its cause nowhere but in the constitution of the living substance of the cell. Need I recall the fact that there are eggs in which this long period of ontogenetic divisions is inaugurated without amphimixis—the parthenogenetic eggs? That in some butterflies (*Bombyx mori*, &c.) the majority of the eggs only enter on this stage after fertilisation, but some few without it. And are we to suppose that this difference does not essentially and above all else depend on the "constitution" of the egg—that is, on the character and quantity of its vital parts? And is the period of activity, beginning with fertilisation and ending with death, to be limited, not only as to its character, but also in its duration, by something external?

Mr. Spencer finds a contradiction in my saying, on the one hand, that the regulation of the duration of life in different species is dependent on things external, while, on the other hand, I refer it to internal characters of cells. But when a king commands a fleet to go to sea, is it *he* who provides the ships with coal, with crews, with provisions; who seeks out the right people, and fixes on the right place; who chooses the ships, determines the course, or makes the machinery, and puts it together, &c.? Of course not; and the king corresponds to the external life-conditions; it is they that give the command: this species shall have an existence of two, of ten, of a hundred years; but the means by which this order is executed consist, in my opinion, above all in the regulation of the life of the cell. It is easy to misunderstand, when one wishes to do so (*Cf.* "Spencer's Appendix," p. 748.)

The division of labour in the metazoan body has brought it to pass that many gland-cells and epithelial cells destroy themselves by their own function, and so they must be continually replaced. We do not yet know with certainty to what extent other highly differentiated cells, such as muscle and nerve-cells, are liable to the same fate, but that they are worn out through exercising their functions is very probable. Now, my hypothesis consists in this: I assume that the restitution of the somatic cells that perish through their activity is arranged for among all species, and depends on modifications in their constitution. As reproduction is a function, just as much as the providing of food, it too will require to be controlled by the constitution of the cell—*i.e.*, with similar nourishment, &c., one kind of cell will reproduce itself more rapidly than another, and the process of reproduction will come to an end earlier in the one, later in the other.

The somatic cells in general, through being specially adapted for a definite function, have lost the power of unlimited reproduction. It was because unlimited power of reproduction was no longer required in them for the maintenance of the species that they were able to assume a high degree of differentiation. In Essay XI.* I say:

"I believe that I have shown that organs which have ceased to be useful become rudimentary, and ultimately disappear, owing to the principles of Panmixia alone—not because of the direct effect of disuse, but because natural selection no longer maintains them at their former level. What is true of organs is also true of their functions; for function is but the expression of certain peculiarities of structure, whether we can directly perceive the connection or not. If, then, the immortality of unicellular beings rests on the fact that the structural arrangement of their substance is so accurately adjusted that the metabolic cycle always comes back to the same point—*why should, or, rather, how could, this property of the protoplasm, which is the cause of immortality, be retained when it ceased to be necessary?* And, clearly, it is no longer of use in the somatic cells of Heteroplastids."

I would now add this: But, wherever it was required, as in the cells that give rise to buds, it had to be retained, and wsa retained.

I would further add that there has been loss of unlimited division of cells, not only through their higher histological differentiation, but wherever it was not necessary or advantageous, which corresponds to the principle of Panmixia. Thus, for instance, we can explain the observations of Klein, the botanist, which are mentioned in Essay XI.† It appears that in one of the lowest Heteroplastids—namely *Volvox*—the body-cells die when the reproductive cells are discharged, even though the somatic cells are quite independent as regards nutrition, and the external conditions are the same before and after the discharge of the reproductive cells. Yet the somatic cells perish, and multiply no further. My opponent may well find it difficult to make one of his nine causes of cell-restriction responsible for this; while my view that the somatic cells are conditioned by their own constitution can hardly meet with any well-grounded opposition.

Mr. Spencer comes to the conclusion, and, in a sense, it is as to the crowning proof of all that he returns to the transmission of acquired characters, and produces, as evidence for its occurrence, those doubtful instances in which the offspring is said to resemble not the father, but an early mate of the mother. If my critic had been better acquainted with my recent book, he would have found that I had not overlooked these instances, and that I had dealt with them in a special chapter, describing them as cases of *telegony*,‡ as no useful term had up to that time been applied to them. They had

* English Translation, vol. ii. p. 76.
† "Aufsätze," p. 646; English Translation, vol. ii. p. 77.
‡ "Das Keimplasma," p. 505; English Translation, p. 383.

previously been referred to as instances of "infection of the germ," or "superfœtation."

I, too, have heard of many such "cases"; for instance, many years ago a doctor from New Orleans gave me the same assurance as to the mingling of negroes and whites that Mr. Spencer has had from a "distinguished correspondent" in the United States. But as long as we have no better data than such as "*on dit*" supplies, we cannot regard telegony as a fact. There are so many possibilities of deception slipping in that we cannot hold it as certain and a basis for scientific conclusions without convincing experiments. Therefore in my book I have called for such experimental work, and specially in zoological gardens, where the requisite care and supervision can be given for long periods, more readily than in small zoological institutes such as my own.

Mr. Spencer assumes telegony to be already demonstrated, and considers it "an absolute disproof of Professor Weismann's doctrine that the reproductive cells are independent of, and uninfluenced by, the somatic cells." He thinks that by this fact every obstacle that is in the way of the acceptance of the transmission of acquired characters is set aside.

But let us see how Mr. Spencer comes to claim telegony as evidence for the transmission of acquired characters. According to his opinion these cases show "that while the reproductive cells multiply and arrange themselves during the evolution of the embryo, some of their germ-plasm passes into the mass of somatic cells constituting the parental body, and becomes a permanent component of it. Further they necessitate the inference that this introduced germ-plasm, everywhere diffused, is some of it included in the reproductive cells subsequently formed." I do not understand what facts Mr. Spencer could rely on when he represented the germ-plasm as passing from the cells of the embryo to those of the mother. The mammalian embryo is only brought into close contact with the maternal tissues by the placenta. Are we to suppose that the cells of the placenta contain germ-plasm? But I am forgetting that Mr. Spencer takes his stand on the assumption of perfectly identical "physiological units"; which, however, have not yet been shown to be capable of furnishing an explanation of the differentiations in the structure of the body. A simpler suggestion would have been that some of the sperm cells had penetrated into the tissues of the mother. This would at least assure the presence of the paternal germ-plasm; but even this supposition is not in accordance with facts, as we know that sperm-cells are strongly attracted to egg-cells, but not to any other kind. Mr. Spencer's idea that the paternal germ-plasm enters from the embryo into the cells of the mother—we may suppose through the maternal placenta—and distributes itself through the entire mass of the somatic cells of the mother's body is so fantastic that I may well say with Mr. Spencer: "Let us not be content with words but look at the facts!" The facts, however, on which he relies are without evidence in connection with this question. It is true that Sedgwick has observed that the cells of *Peripatus* embryos form a so-called *syncytium*, that is that the cells are not apparently distinct from one another; and it is also well known that both among plants and animals the cells of some or many of the tissues are connected by protoplasmic threads, but these facts do not prove that germ-plasm is transported from cell to cell. If it is shown that a highway leads from London to Oxford, this is not sufficient to prove that Peter has taken it.

If Mr. Spencer had even glanced at my Essays V., VI., and XII., it would have been inexplicable how he could so completely have ignored in his hypothesis the researches of the last ten years on the microscopic relations of the cell-nucleus. We have now abundant facts to enable us to conclude with certainty that the hereditary substance is contained in the nucleus of the germ-cell, that it is in a manner shut up there, and carefully preserved; and that it never as a whole leaves the nuclear capsule. When it is to be shared with another cell, this is effected by the method of nuclear and cell division. The cell contains for the purpose a special apparatus of marvellous delicacy and precision, whose wonderful mechanism is still the subject of eager study by our best microscopists, both in the sphere of botany and zoology. *Of what use would all this dividing apparatus be, if the hereditary substance could quite as well be transmitted from cell to cell through the cell-bodies?* Investigation has also established that the mingling of the hereditary substance of two cells produced by different parents is brought about by a specially developed process, which I have designated amphimixis, and which, so far as we know, occurs regularly only as conjugation among the unicellular organisms and as fertilisation among multicellular forms. But among the higher plants it occurs also as a regular phenomenon in other cells, namely, in a certain pair of nuclei of the so-called embryo-sac. It is not at all impossible that amphimixis occurs elsewhere, though perhaps only exceptionally, that is, in quite unusually favourable circumstances; and I have made the attempt to explain in this way the origin of the "graft-hybrids"—*e.g.*, of the celebrated *Cytisus Adami*. From the fact that hereditary substance (idioplasm) is found only in the nuclear rods, and "is a solid substance, and can only undergo combination by the fusion of two cells and their nuclei," * I concluded that amphimixis of two cambium cells of two species must be the cause of the graft-hybrids; but I added that here "an unusual and accidental occurrence" must have regulated the formation of such a mongrel-bud "for all efforts to produce the hybrid a second time have so far been in vain."

* "Keimplasma," p. 447; Eng. Ed. p. 341.

But though we may suppose that in specially favourable circumstances, amphimixis may occur between two cells other than germ-cells, it would nevertheless not be permissible to assume that this is frequent, and is found in all kinds of somatic cells, or even in all the cells of the body, and continually; as must be believed if Spencer's theory of the transmission of germ-plasm from the embryo all through the body of the mother is really correct. Such a distribution as he imagines, which is independent of amphimixis, and proceeds only by transmission through the protoplasmic threads from cell to cell, is in hopeless contradiction to the facts just stated. Nature has carefully enclosed the germ-plasm of all germ-cells in a capsule, and it is only yielded up for the formation of daughter-cells, under most complicated precautionary conditions, or in unions with other cells, under the form of amphimixis. This gives us no right to suppose that germ-plasm can, like a flock of birds, spread out over the whole body from cell to cell, so long as there is no other reason for the supposition than that the hypothesis of the transmission of acquired characters can thereby be made plausible.

So when Mr. Spencer produces "as a sample of his (*i.e.*, my) reasoning" the fact that, on the one hand, I grant that the micro-organisms of syphilis or those which I assumed to be the cause of traumatic epilepsy may pass from a body infected by one of these diseases into the germ-cells of the body, while, on the other hand, I do not admit the "parental protoplasm" there, he forgets that the infection of the germ by syphilis is a demonstrated fact, while vagrant germ-plasm has never been found permeating the mother's body; and to assume it is to scorn all research on the transmission of the germ-plasm from cell to cell. There is no doubt that a murderer may travel from London to Paris, just like any other man; but when he has been shut up in prison, it is not so easy; he must first break loose from confinement. Even so the germ-plasm seems to be able to wander only under quite definite conditions, while the free microbe passes unimpeded along the streams of blood and sap, and, it may be, from cell to cell, through the whole body.

Mr. Spencer's explanation of telegony is thus altogether inadmissible, and the fact itself, far short of being "an absolute disproof" of my views, can at least much more easily be brought into harmony with them in the event of its being proved to actually occur. In my "Germ-Plasm" I have already attempted to explain it; and my explanation follows so simply and naturally from my views on germ-plasm, amphimixis, &c., that Prof. Romanes, without having seen my book, was able, when replying to Mr. Spencer in this REVIEW, to suggest as my probable response to Spencer's argument an answer that, in the main, quite conforms with what I had actually written. I also gave the same explanation of telegony in 1887, when I was asked in the Biological Section of the British Association Meeting at Manchester, how I could reconcile such cases with my theory. There is no simpler supposition than that spermatozoa occasionally reach the ovary, and there enter into some of the immature eggs. Amphimixis cannot proceed, as the germ-plasm of the egg is not ripe, but the nucleus of the sperm-cell continues to live in certain circumstances, and so remains till the time of a subsequent *coitus* with another mate. "If this occurred some time after the first of the offspring was born, it might easily have coincided approximately with the second coitus, to which the fertilisation would then apparently be due."

With this indication of an explanation I thought to be content and went on as follows:

> "If the 'infection' were proved beyond a doubt, a supplementary fertilisation of an egg-cell in this manner must be considered possible; we certainly might then reasonably ask why mares, cows, or sheep, should not occasionally become pregnant without being covered a second time. *But this has never yet been known* to occur, and I incline to Settegast's view that *there is no such thing* as an 'infection' of this kind, and that all the instances which have been recorded and discussed critically by him are based upon a misconception." *

I must say that to this day, and in spite of the additional cases brought forward by Spencer and Romanes, I do not consider that telegony has been proved—even though I thus lay myself open to Mr. Spencer's suspicion that I am not only ready "to base conclusions on things it is easy to imagine" but "reluctant to accept testimony which it is difficult to doubt." I do not dispute the possibility of telegony; I grant that the wide general acceptance of the belief in the past has so impressed me that I have always said that possibly it might be justifiable and founded on fact. In like manner the "rust" of corn (*Puccinia graminis*) was regarded by peasants as being somehow caused by the barberry, long before De Bary succeeded in raising the tradition to the rank of a scientific fact, by showing that the fungus on the corn and the *Æcidium berberidis* on the leaves of the barberry are the alternate generations of one plant. So I consider it inexpedient to reject such popular traditions without consideration; and I should accept a case like that of Lord Morton's mare as satisfactory evidence, if it were quite certainly beyond doubt. But that is by no means the case as Settegast † has abundantly proved. He does not doubt that "after the mare had borne a hybrid to a quagga, she subsequently had colts by a horse, and that these were marked with stripes on the neck, withers, and legs"; but he contends that there were no other characteristics of the quagga discernible in the colts: in the drawings by Agasse in the Royal College of Surgeons, London, "the liveliest imagination would not avail to find any semblance to the form of the quagga." The stripes do not in them-

* "Keimplasma," p. 507; Eng. Ed., p. 386.
† H. Settegast: "Die Thierzucht": Breslau, 1878. Vol. i. p. 225.

selves, Settegast thinks, amount to proof, "for every experienced horsebreeder knows" that "cases are not very rare in which colts are born with stripes that recall those of the quagga or zebra. They regularly disappear as the colts increase in age." Such an experienced breeder as Nathusius remarks as to this:

> "A spotless light brown mare that I had, whose sire was Dan Dawson, produced first, one after another, five spotless colts by the thoroughbred stallion Belzoni, and subsequently two spotless colts by the trotting-horse Schultz; the eighth colt, whose sire was a white horse, Chiradam, was at its birth of a dusky dun colour, with dark stripes on the back; and on the knee and hock it showed dark zebra-like bands which were much more distinct than those that occurred on Lord Morton's colt; but in a year these marks had disappeared, and the horse was white like its father."

Moreover, experiments have been made with a view to proving the occurrence of telegony, as I see from a note in Settegast's book (p. 226). A Herr Lang of Stuttgart has for twenty years experimented with dogs, without, however, ascertaining "a single fact that could be made use of for the advancement of the infection theory." Of course, in such a case negative results prove nothing; and the attempt must be made to determine the truth by new experiments. But as hitherto there have been no positive results from the observations that have been made; and as the most competent judges, namely, breeders who have a scientific knowledge, such as Settegast and Nathusius, and the late head of the Prussian Agricultural Station at Halle, Professor Kühn, spite of their extensive experience in breeding and crossing, have never known a case of telegony, and therefore have great doubt as to its reality; it seems to me that *according to scientific principles, only the confirmation of the tradition by methodical investigation, in this case by experiment, could raise telegony to the rank of a fact.*

With this I may close my reply to Herbert Spencer, though he has stated several other objections, which it would not be uninteresting to discuss. But the space at my disposal is limited, and the questions at issue involve many considerations, and cannot be disposed of in a few words. I hope to return to them in a subsequent treatise. If I have not the good fortune to convince my opponent—the usual event of controversial encounters—perhaps, at any rate, the unbiased reader will grant that my opinions are not without foundation; and I am content to leave the future to decide whether, and how far, they will become an indisputable and sure possession of science. They have already borne good fruit, for they have opened up new fields fo research; and it is my hope that they will continue to stimulate progress.

AUGUST WEISMANN.

SCIENCE AT CAMBRIDGE,

BY

DR. MONCKMAN.

(Of Downing College.)

CAMBRIDGE—DEIGHTON, BELL, & CO., TRINITY STREET.

BRADFORD—HONORARY SECRETARIES OF THE SCIENTIFIC ASSOCIATION,—MR. J. SKELTON, CROSSLEY HALL; MR. WM. PICKLES.

1888.

SCIENCE AT CAMBRIDGE,

BY

DR. MONCKMAN.

(Of Downing College.)

PRICE 3D.

CAMBRIDGE—DEIGHTON, BELL, & CO., TRINITY STREET.

BRADFORD—HONORARY SECRETARIES OF THE SCIENTIFIC ASSOCIATION,—MR. J. SKELTON, CROSSLEY HALL; MR. WM. PICKLES.

PREFACE.

—:-o-:—

DR. MONCKMAN ON THE TEACHING OF SCIENCE AT CAMBRIDGE.

IN a lecture delivered on Jan. 6th, before the Bradford Scientific Association on "Science at Cambridge," Dr. Monckman said that there was a tendency to regard as education the mere learning of scientific facts. This being produced partly by the muliplicity of books, but more by the present system of preparation for examinations, especially those on which money is paid to the teachers of successful candidates. Such a method of acquiring information cannot be regarded as education in any sense, much less as scientific education, which may be defined as "Training the mind to accurate observation of natural phenomena." The system used in the University of Cambridge may be stated briefly thus. Thorough teaching by lectures, demonstrations, and practical work, with an abundance of apparatus and careful supervision to ensure that the students not only get the information, but that they get it properly and make it a means of mental improvement and not of cram. The advanced students are encouraged and assisted in carrying out original investigations, and so great has been the success of the system employed that the lecturer was able to present a list of 270 papers on research work published by members of the University during the years 1886 and 1887.

On the motion of J. Beer, F.S.A., seconded by W. West, F.L.S., a hearty vote of thanks was given to Dr. Monckman.

T. H. SKELTON, } Hon. Secretaries.
W. PICKLES, }

An idea commonly prevails that the Universities of Cambridge and Oxford spend the whole of their endowments in promoting the study of Classics and allied subjects. That this is so among the grossly ignorant only, can scarcely be maintained, when the Member for Bradford, the Right Honourable Shaw-Lefevre, a member of the University, actually knew so little of the progress of Science at Cambridge as to venture upon embodying it in words in a recent address to a portion of his Constituents.

Thirty years ago it was true enough but since that time a great change has been gradually taking place. In 1851 the Natural Science Tripos was instituted for the purpose of giving encouragement to the pursuit of certain branches of Natural Science, which had not before been recognised among the studies of the place. The subjects of examination are Chemistry, Physics, Geology, Mineralogy, Botany, Zoology, Anatomy—Human and Comparative, and Physiology. "The examination is divided into two parts. In Part I. the questions are of a comparatively elementary character testing a knowledge of principles rather than details. Part II. is for those Candidates only, who have succeeded in passing Part I. and is intended to test not so much the range of their knowledge as its thoroughness. In 1886, 91 Degrees were conferred on students passing the Science Tripos, while Classics took 108 and Mathematics, 113.

During the same period there has also grown up one of the finest collections of Laboratories devoted to the thorough practical study of Science. Situated in a central position, within five minutes' walk of the majority of the Colleges, they occupy a space of about 8000 yds, and are supplied with the apparatus and specimens necessary for the study of the various branches of Science to which they are devoted. Over them preside 13 Professors.

The teaching is thorough and practical, entirely opposed to the modern system of cramming. The words of Prof. Liveing will show the idea on which it is based; he says:—"No student can get adequate conceptions of Physical Facts so as to be able to reason upon them with certainty, unless he himself has observed them." So great has been the success that all the departments are out-growing their space, and some of them strongly remind us of the big boy whose legs are too long, and whose coat sleeves too short. This has, until now, been the case with the Chemical Department. A new Laboratory has just been finished, and is said, by competent judges, to be the most complete, though not the largest, in Europe. Prof. Stuart is striving to achieve the same result for the Engineering, for which the Senate are now discussing a scheme for holding a Tripos.

The members of the University are allowed access to the following Institutions:—(1) The University Library; (2) Philosophical Library; (3) Fitzwilliam Museum; (4) Woodwardian Geological Museum; (5) Museum of Zoology and Comparative Anatomy; (6) Minerological Museum; (7) Observatory, &c.

At all the Colleges except Corpus, Trinity Hall, Magdalene, and Pembroke, Scholarships for Natural Science, and in some, Fellowships are awarded for proficiency in the same subject. Prizes in money are given, and in some subjects travelling Scholarships, to enable students to procure further information, or to pursue sôme special investigation abroad.*

There are now in residence, 10 Science Scholars in one College whose number is under 200. This however is one of the best Colleges in the University in respect to Science.†

Not only by the number of Students is the success of the teaching shown, but also by the fact that the mental training qualifies many for original research.

The extent to which the country is indebted to the endowments of the University, for investigations of this kind may be, in some measure estimated from the following list of Original Papers, published by resident members of the University during the years 1886 and 1887.

EVERY effort has been used to make the list complete for the two years, some important papers of an earlier date are included.

It is hoped that others may be induced to continue the list yearly, so that eventually it may prove a most convenient means of reference, to students engaged in original investigation.

---

* See the Schoolmaster's Calendar and Hand-book of Open Scholarships, published by George Bell & Son, York Street, Covent Gardens. Information may be obtained from the Tutors of the Colleges, &c.

† For further information on Examinations, Hand-books, College Expenses, &c., consult the Student's Guide to the University of Cambridge, published by Deighton Bell & Co., Cambridge.

ASTRONOMY.

SUBJECT.	AUTHOR.	WHERE PUBLISHED.
On the Correction to the Equilibrium Theory of Tides for Continents. Part I.	*Prof. G H. Darwin, L.L.D., F.R.S.*	Pr. Roy. Soc. April, 1886.
Part II.	*H. H. Turner, B.A. (Now First Assistant at Greenwich.)*	,,
On the Dynamical Theory of Tides of Long Period.	*Prof. G. H. Darwin, L.L.D., F.R.S.*	,, Nov. 1886
On Jacobi's Figure of Equilibrium of a Rotating Mass of Fluid.	,,	,, October, '86
Fourth Report of Committee for Harmonic Analysis of Tidal Observations.	,,	B.A. Report, 1886
Articles on Tides	,,	Admiralty Scientific Manuel, 1886 Encyclo. Britan. 1887
Note on Mr. Davison's paper on the Straining of the Earth's Crust in Cooling	,,	Phil. Trans., read, June 16, 87
On the Forms of Equilibrium of a Rotating mass of Fluid	,,	Read, June, 1887
Earthquakes	,,	Fortnightly Review Feb. 87

BOTANY.

Note on the Vesicular Vessels of the Onion.	*Dr. Vines and A. B. Rendle, B. A.*	Camb. Phil Socy. Proc.
On Epiclemmydia Lusitanica, a new Genus of Algæ.	*M. C. Potter, M. A.*	,, (& Jour. Linn. Soc.
On a peculiar Organ of Hodgsonia Heteroclita.	*W. Gardiner, M. A.*	,,

On the structure of Mucilage-secreting Cells of Blechnum.	*W. Gardiner & T. Ito*	Ann. of Botany
The Transpiration of the Sporophore of the Musci.	*J. R. Vaizey*	„
The Constitution of the Cell-Walls of Mosses in their relation to Absorption.	„	„
On the Anatomy and Development of the Sporophore of Mosses.	„	Jour. Linn. Soc.
The Effect of Stimulation on Vegetable Tissues.	*F. Darwin and Miss Bateson*	„ „
On the Chemical changes taking place in Germinating Seeds.	*J. R. Green, B. Sc., B.A.*	Phil. Trans.
On Alternation of Generation in Plants.	*J. R. Vaizey*	British Association
On the Process of Secretion in Plant Cells.	*W. Gardiner*	„
On Nitrogenous Nutrition of Plants.	*Dr. Vines*	„
On the Mechanism of the Movement of the leaves of Mimosa Pudica.	„	„
Effect of Stimulating the Gland-Cells in Tentacles of Drosera dichotoma	*W. Gardiner, M.A.*	39—229

CHEMISTRY.

On the Volumetric Determination of Chromium.	*W. J. Sell, M.A.*	Chemical News, Dec. 86
On the Limited Hydration of Ammonium Carbamate.	*H. J. H. Fenton, M. A.*	Roy. Socy. 1885
Case of so-called Catalytic Action.	„	Camb. Phil. Socy. March, 1885
Some Observations on Permanganic Acid.	*T. H. Easterfield, B.A.*	„ Oct. 87

Redetermination of the Atomic Weight of Cerium.	*H. Robinson, M.A.*	Pro. Roy, Socy. 84
Colour of the Oxides of Cerium and its Atomic Weight.	,,	British Assoc. 1886
Spectrum (absorption) of Praseodym and Neodym, also of Didymium.	,,	,,
The Analysis of Crystals of Apatite.	,,	Journal of Mineralog. Soc. Vol. vii. No. 33
Second paper on the same.	*H. Robinson, M.A.*	Trans. Roy. Geolog. Soc. Cornwall, 1886
On a New Form of Direct Vision Spectroscope.	*Prof. Liveing, F.R.S., and Prof. J. Dewar F.R.S.*	Pro. Roy. Soc. Nov. 1885
On the Influence of Capillary Action on some Chemical Decompositions	*Prof. Liveing*	Camb. Phil. Socy. Nov. 86
On a Fall of Temperature resulting from an increase in the supply of Heat.	,,	,, Eeb. 86
On the Constitution of Pyridine, &c.	*Dr. Ruhemann*	Jour. Chem. Soc. May, 87
Anacardic Acid.	*Dr. Ruhemann, and S. Skinner, B.A.*	,, Aug. 87
Phosphonium Chloride.	*S. Skinner, B.A.*	Pro. Roy. Soc. V. 2
On the action of Ammonia on the Ethereal Salts of Fatty Oxyacids.	*Dr. Ruhemann*	Chem. Jour. June, 87
On the action of Phenyl Hydr, on the Urea Derivatives.	*Dr. Ruhemann, and S. Skinner, B.A.*	Chemical Jour. 1887
On Bismuthates.	*M. M. Pattison Muir, M.A. and D. Carnegie, B.A.*	Chem. Soc. Jour, 1887
On Periodates.	*Dr. C. W. Kimmins*	,,
Interaction of Zinc and Sulphuric Acid.	*M. M. Pattison, Muir, M.A. and R. H. Adie, B.A.*	,,
Bismuth Iodide and Fluoride.	*M. M. Pattison, Muir, and B. S. Gott, B.A.*	

GEOLOGICAL PAPERS.

On the Decapod Crustaceans of the Oxford Clay.	*James Carter*,	Q.J.G.S. p. 542. 1886,
On some Perched Blocks, and Associated Phenomena.	*Prof. T. McK. Hughes*	Q.J.G.S. 1886.
On the Ffynon Beuno Caves.	*Prof. T. McK. Hughes*	Geol. Mag. 1886, p. 489.
On the Silurian Rocks of North Wales.	„	Brit. Assoc, 1886.
Notes on some Sections in the Arenig Series of North Wales, and the Lake District.	„	Brit. Assoc. 1886.
On the Pleistocene Deposits of the Vale of Clwyd.	„	Brit. Assoc. 1886.
On the Drifts of the Vale of Clwyd, and their Relation to the Caves and Cave-deposits.	„	Q.J.G.S, 1887, p. 73.
On the Ancient Beach and Boulders near Braunton and Croyde in Devon.	„	Q.J.G.S. 1887, p. 657.
On the Correlation of the Upper Jurassic Rocks of the Swiss Jura with those of England.	*Thomas Roberts, M.A.,F.G.S.*	Q.J.G.S. 1887, p, 229.
The Rocks of Sark, Herm, and Jethou.	*Rev. E. Hill, M.A.F.G.S.*	Q.J.G.S. 1887, p, 322.
On Pelanechinus corallinus.	*T. T. Groom*,	Q.J.G.S. 1887.
Woodwardian Museum Notes. On some Anglesey Dykes, I.	*A. Harker, M.A.F.G.S.*	Geol. Mag. 1887, p, 409.
Woodwardian Museum Notes. On some Anglesey Dykes, II,	„	Geol. Mag. 1887, p, 546.
In Brittany with the Geological Society of France.	*Rev. E. Hill, M.A.,F.G.S.*	Geol. Mag. 1887, p, 500,
On some Breciated Rock in the Archaean of Malvern.	*Prof. T. McK. Hughes*,	Geol. Mag. 1887, p, 500.

Bursting Rock Surfaces.	,,	Geol. Mag. p, 511.
On the Discovery of the Nummulina elegans Zone at Whitecliff Bay, Isle of Wight.	*H. Keeping*,	Geol. Mag. 1887, p, 70.
On some sections of the Neocomian in Lincolnshire.	*H. Keeping*	Geol. Quar. Jour. 1882
The Lower Palæozoic Rocks, near Settle.	*J. E. Marr, M.A., F.G.S.*	Geol. Mag, 1887, p, 35.
The Work of Ice Sheets.	,,	Geol. Mag. 1887, p, 151.
On the Glacial Deposits of Sudbury.	,,	Geol. Mag. 1887, p, 262.
On Homotaxis.	,,	Proc. Camb. Phil. Soc. 1887.
On Slaty Cleavage and Allied Rock Structures	,,	Brit. Assoc. 1886, p, 813

LIST OF SEDGWICK PRIZE ESSAYS.

1873, The Potton and Wicken Phosphatic Deposits.	*J. J. H. Teall*,	1875
1876, The Post-teritary Deposits of Cambridgeshire.	*A. J. Jukes Browne*,	1878.
1879, The Fossils and Palæontological Affinities of the Neocomian Deposits of Upware, and Brickhill	*Walter Keeping*,	1883
1882, The Classification of the Cambrian and Silurian Rocks.	*J. E. Marr*,	1883.
1886, The Jurassic Rocks of the neigbourhood of Cambridge,	*T. Roberts*,	Not Pub.

MINERALOGY.

Notes on Minerals from Devonshire and Cornwall.	*R. H. Solly.*	Mineralog. Jour. Vol. vi. P. 202

Francolite, a Variety of Apatite from Cornwall.	*R. H. Solly*	,, Vol. vii. P. 57
Anglesite from Portugal.	,,	,, Vol. vii. P. 61
Apatite from new locality in Eastern Cornwall.	,,	,, ,, P. 141
Celestine from a new locality in Gloucestershire.	,,	,, ,, P. 142

PHYSICS.

On the action of the solvent on Electrolytic Conduction.	*T. C. Fitzpatrick, B.A.*	Phil. Mag. Nov. 1887
Effect of Polish on the Reflexion of Light from the surface of Iceland spar.	*C. Spurge, B.A.*	Pro. Roy. Socy. 32, P. 242
Conduction of Heat in Liquids.	*C. Chree, M.A.*	Pro. Roy. Socy. 42, P. 30
Do. Historical Inquiry.	,,	Phil. Mag. July '87
A new Solution of the Equations of an Isotropic Elastic Solid.	,,	Journal Pure & App. 1886
Certain forms of Vibration.	,,	Pro. Edin. Math. Soc. Vol. iv. S 85 & 6
Longitudinal Vibrations of a Circular Bar.	,,	Jour. P. & A. Math. 1886
Bars and Wires of Varying Elasticity.	,,	Phil. Mag. Feb. & Sept. 1886
Vibrations of a gas included between two Concentric spherical surfaces.	,,	Messen. Math. June '85
On the Form in Polar Co-ordinates of certain expressions in Elastic Solids.	,,	Pro. Edin Math, Soc, 1885
Elastic Solids forming parallel Strata.	,,	Jour. Math. Soc. 1885 & 6
Elastic Solids of Varying Elasticity.	,,	,,

Vortices.	*C. Chree, M. A.*	Pro. Edin. Math. S. Feb. 1887
A New Method of producing the Fringes of Interference.	*L. R. Wilberforce, B.A.*	Camb, Phil. Soc. Vol. V. 325
On a Method of Measuring Specific Inductive Capacity.	„	„
Some Experiments on the Measurement of Capacity of Condensers.	„	„ 175 & 182
On the Practical Measurement of Temperature.	*H. L. Callendar, B.A.*	Phil. Trans. Roy. Soc. 87
Effect of Moisture in Modifying the Refraction of Plane Polarized Light by Glass.	*R. T. Glazebrook, F.R.S.*	Pro. Camb. Phil. Soc. Vol. V. 169
On the Theory of some Experiments of Fröhlich on the position of the plane of polarization of Light diffracted at reflexion from a grating.	„	„ Vol. V. 254
On Young's Eriometer.	„	„ Vol. V. 223
A comparison of the B.A. Standard Resistance Coils with Mercury standard.	„	Phil. Mag. xx. 343
Measuring the Electrical Capacity of a Condenser.	„	
Determining by Electrical Observations of the Period of a Tuning Fork.	„	Do. 18. 98
Report on Optical Theories.	„	B.A. Report, 1885
On an Experiment on Ventilation.	*W. N. Shaw, M.A.*	Camb. Phil. Soc. Vol. V. 410
On some Measurements of the Frequencies of the Notes of a Whistle of adjustable pitch.	*W. N. Shaw, M.A. and F. M. Turner.*	„ 90
On the Atomic Weights of Silver and Copper.	*W. N. Shaw, M.A.*	Phil. Mag. 23, 188

Note on the Rotation of the Plane of Polarization of Light by a moving medium.	*Prof. J. J. Thomson, F.R.S.*	Pro. Camb. Phil. Soc. V. 250
On the Electric Discharge in a Uniform Electric Field.	*Prof. J. J. Thomson, F.R.S.*	" V. 391
On the Stability of Motion of a Viscous Fluid.	"	"
Report on Electrical Theories	"	B.A. Report, 1885
On the Application of Dynamical Principles to Physical Phenomena (Pt. I.)	"	Phil. Trans. Roy. Socy. 85
" " (Part II.)	"	" 87
Vortex Ring Theory.	"	Pro. Roy. Soc. 1885
On the Dissociation of some gases, by the Electric discharge.	"	Pro. Roy. Socy, 43, 343.
On Electrical Vibrations in Cylindrical Conductors.	" "	Pro. London Math. Socy., June, 86
On the Passage of the Electric Discharge through pure Nitrogen and some experiments on the Production of Ozone.	" *(and Prof. Threlfall)*	Pro. Roy. Socy. 40, 329
On the Production of Vortex Rings by drops falling into a liquid.	*Prof. Thomson, and H. F. Newall, M. A.,*	" 39, 417.
On the Rate at which Electricity leaps through liquids which are bad Conductors.	"	" 42, 410
On some experiments in Magnetism	*H. F. Newall, M,A.*	Cam. Phil. Socy., V. 1
Peculiarities observed in Iron and Steel, at a bright red heat	"	Phil. Mag. Nov. 87
On Experimental Investigation into the form of the wave surface in Quartz.	*J. C. McConnell*	Phil. Trans., 1886
Relation between Surface Tension Chemical Action.	*Prof. Thomson and Dr. Monckman*	Camb. Phil. Socy, Nov. 87

PHYSIOLOGY.

On the Augmentor Nerves in the Heart of Cold-blooded Animals.	*W. H. Gaskell, M.D.,F.R.S.*	Journal of Physiology, Vol. v., p. 46
On thé Anatomy of the Cardiac Nerves in Certain Cold-blooded Animals.	*Dr. Gaskell and Hans Gadow, Ph.D.*	,, 236
Action of the Sympathetic Nerves upon the Heart of the Frog.	*Dr. Gaskell*	,, xiii
The Structure, Distribution, and Functions of the Nerves, which innervate the Visceral and Vascular Systems.	,,	,, Vol. vii, p. 1
Electrical changes in Quiescent Cardiac Muscle which accompany stimulation of the Vagus Nerve.	,,	,, p. 451
Secondary Degeneration of Nerve Tracts, following removal of Cortex of Cerebrum in the Dog.	*J. N. Langley, M.A.,F.R.S., and C. S. Sherrington, B.A.,*	,, Vol. v, p. 49
The Paralytic Secretion of Savlia.	*J. N. Langley, M.A.,F.R.S.*	,, vi. p 71. & Pro. Roy. Soc., 38,212
Distribution of Fat in the Liver Cells of the Frog.	,,	Pro. Roy. Soc. No. 39, p. 234
Structure of Mucous Salivary Glands.	,,	No. 40, p. 362
Pepsinogen and Pepsin.	,, *and J. S. Edkins, B.A.*	Phy. Journ. vii p. 371
On Hypnotism	,, *H. E. Wingfield, M.A.*	,, xvii.
Observations on the Gastric Glands of the Pig.	*Miss M. Greenwood*	Jour. of Phy. Vol. V. p. 195 & vii
Digestive Process in some Rhizopods.	,,	viii. 235 & 263 also vii., 253

Comparison of the concentration of Solutions of different strengths of the same absorbing substance.	*Sheridan Lea, Sc.D.*	Jour. of Phy. V. p. 239
The action of Rennet Ferment contained in the seeds of Withania.	,,	,, vi.
A new Absorptiometer.	,,	,, xii
The Isolation of a Soluble Urea from Torula Ureœ.	,,	vii—136
The Liver Ferment.	*Florence Eves, B.Sc.*	v—342
The Edible Bird's Nest.	*J. R. Green, B.Sc., B.A.*	vi—342
Proteid substances in Latex.	,,	Pro. Roy. Soc. 40, 28
Changes in the Proteids of seeds which accompany Germination.	,,	,, 41—466
Influence of Glycerine on the Liver.	*W. B. Ranson, M.A.*	Jour. of Phy, viii—99
On the Endocardial Pressure Curve.	*H. B. Rolleston, B.A.*	viii—235
On the Origin of Respiratory Sounds.	*J. F. Bullar, M.B.*	Pro. Roy, Soc. No. 37—41
Influence of Bodily Labour on the discharge of Nitrogen.	*W. North, B.A.*	No. 39—443
Pathology of Cholera Asiatic.	*C. S. Roy, F.R..S, and Dr. J. G. Brown*	No. 41—173
Variations in Specific Gravity of Blood	*E. Lloyd Jones*	Jour. of Phy. p. 1, Vol. viii

ZOOLOGY, AND COMPARATIVE ANATOMY.

Origin of Suprarenal Bodies in Vertebrates.	*W. F. R. Weldon, B.A.*	Pro. Roy. Socy. 37—422
A Balanoglossus Larva, from the Bahamas.	,,	42—146
The Developement of Peripatus Capensis.	*A. Sedgwick, M.A.*	38—354
Fertilised Ovum of the South African Peripatus.	,,	39—244
On the Development of the Mole.	*Walter Heape, M.A.*	Quarterly Journal of the Microscopical Society, 1886
Development of Peripatus.	*Adam Sedgwick, M.A.*	,,
Development of Iulus Terrestris.	*F. G. Heathcote, M.A.*	,,
Note on the presence of a Neurenteric Canal in Rana.	*H. E. Durham*	,,
Continued Account of the later stages of Development of Balanoglossus.	*W. Bateson, M.A.*	,,
The Ancestry of the Chordata.	,,	,,
Note on the Development of Triton.	*Alice Johnson, (Newnham College)*	,,
On Dinophilus Gigas.	*W. F. R. Weldon, M.A.*	,,
Development of the Mole.	*W. Heape, M.A.*	,,
On the Life History of Pedicellina.	*S. F. Harmer, M.A.*	,,
Some points in the Development of Petromyzon fluviatilis.	*A. Shipley, M.A.*	,, 1887
On the Development of Capes Species Peripatus.	*A. Sedgwick, M.A.*	,,
On the Ciliated Pits of Ascidians.	*Lilian Sheldon (Newnham Coll:)*	,,

Development of Peripatus Capensis.	*A. Sedgwick, M.A.*	,,
Monograph of Species and Distribution of Genus Peripatus.	,,	,,
Postembryonic Development of Iulus Terrestris.	*F. J. Heathcote, M.A.*	,,
Development of Peripatus Novæ Zealandiæ.	*Lilian Sheldon (Newnham)*	,,
Development of Peripatus from Demerara.	*W. L. Silater, B.A.*	,,
Development of Monotremata.	*W. H. Caldwell, M.A.*	Phil. Trans. xlii. 177
Appendix to Prof. McIntosh's Report on Cephalodiscus.	*S. F. Harmer, M.A.*	(Challenger Report)

J. Green, Printer, &c., 311, Manchester Rd., Bradford.

14

THE METHOD OF ORGANIC EVOLUTION.

I.

THE modern doctrine of organic evolution may be said to date from the great French naturalist Buffon, who, more than a hundred years before the publication of the *Origin of Species*, clearly indicated his belief in the mutability of specific and generic forms, although, owing to the power of the Church in his day, he was often obliged to veil his opinions under the guise of hypotheses, which, as they were opposed to religion of course could not be true. Yet he occasionally speaks very plainly, as when he says:—

> "Nature, I maintain, is in a state of continual flux and movement;"

and again—

> "What cannot Nature effect with such means at her disposal? She can do all except either create matter or destroy it. These two extremes of power the Deity has reserved for Himself only; creation and destruction are the attributes of His omnipotence. To alter and undo, to develop and renew—these are powers which He has handed over to the charge of Nature."

Dr. Erasmus Darwin held similar views, which he developed at great length, and in doing so, anticipated many of the arguments afterwards elaborated by the celebrated Lamarck, that changes in species were caused both by the direct action of the environment, by the use and exercise by animals of their several organs, and more especially by the effects of effort and desire leading to the development of parts and organs calculated to gratify those desires. The great French naturalists Geoffrey and Isidore St. Hilaire adopted these views with certain modifications, as did a limited number of German naturalists; while they were popularly set forth with much knowledge and literary skill by the late Robert Chambers in his *Vestiges of Creation*. Somewhat later the general theory of evolution was explained and illustrated by Herbert Spencer with so much power and completeness as to compel its acceptance by most thinkers; but neither he, nor any of the great writers who had gone before him, had been able to overcome the difficulty of explaining the process of organic evolution, since no one had been able to show how the wonderful and complex adaptations of living things to their environment could have been produced by means of known laws and through causes proved to exist and to be of sufficient potency. Alike for naturalists, for men of science in general, and for students in philosophy, the *method* of organic evolution remained an insoluble problem.

Considering that this state of opinion prevailed up to the very date of publication of the *Origin of Species*, the effect produced by that work was certainly marvellous. A considerable body of the more thoughtful naturalists at once accepted it as affording, if not a complete solution, yet a provisional theory, founded upon incontrovertible facts of nature, demonstrating a true cause for specific modification, and affording a satisfactory explanation of those countless phenomena of adaptation which every preceding theory had been powerless to explain. Further consideration and discussion only increased the reputation of the author and the influence of his work, which was still further enhanced by his *Animals and Plants under Domestication*, published nine years later; and when this had been fully considered—about twelve years after the publication of the *Origin*—a large proportion of naturalists in every part of the world, including many of the most eminent, had accepted Darwin's views, and acknowledged that his theory of Natural Selection constituted—to use his own words—"the main but not the exclusive means of modification." The effect of Darwin's work can only be compared with that of Newton's *Principia*. Both writers defined and clearly demonstrated a hitherto unrecognised law of nature, and both were able to apply the law to the explanation of phenomena and the solution of problems which had baffled all previous writers.

Of late years, however, there has arisen a reaction against Darwin's theory as affording a satisfactory explanation of organic evolution. In America, especially, the theories of Lamarck are being resuscitated as of equal validity with natural selection; while in this country, besides a considerable number of Lamarckians, some influential writers are introducing the conception of there being definite positions of *organic stability*, quite independent of utility and therefore of natural selection; and that those positions are often reached by *discontinuous variation*, that is, by spurts or sudden leaps of considerable amount, which are thus "competent to mould races without any help whatever from the process of selection, whether natural or sexual."[1] These views have been recently advocated in an important work on variation,[2] which seems likely to have much influence among certain classes of naturalists; and it is because I believe such views to be wholly erroneous and to constitute a backward step in the study of evolution that I take this opportunity of setting forth the reasons for my adverse opinion in a manner likely to attract the attention not only of naturalists but of all thinkers who are interested in these problems.

Before proceeding to this special discussion it may be well to illustrate briefly the essential difference between the theories of

(1) *Discontinuity in Evolution*. By Francis Galton. *Mind*, vol. iii., p. 367.

(2) *Materials for the Study of Variation, treated with especial regard to Discontinuity in the Origin of Species*. By William Bateson, M.A. 1894 (pp. xv. and 598).

Darwin and those of his predecessors and opponents, by a few examples of those cases of adaptation which are insoluble by all other theories, but of which natural selection gives an intelligible explanation.

The Darwinian theory is based on certain facts of nature which, though long known to naturalists, were not understood in their relations to each other and to evolution. These facts are: variation, rapid multiplication, and the resulting struggle for existence and survival of the fittest. Variation is the fundamental fact, and its extent, its diversity, and its importance are only now becoming fully recognised. Observation shows that when large numbers of individuals of common species are compared there is a considerable amount of variability in size, form, colour, in number of repeated parts and other characters. Further, that each separate part, which has been thus compared, varies, so that it may be safely asserted that there is no part or organ that is not subject to continual variation. Again, all these variations are of considerable amount—not minute, or infinitesimal, or even small, as they are constantly asserted to be. And, lastly, the parts and organs of each individual vary greatly among themselves, so that each separate character, though sometimes varying in correlation with other characters, yet possesses a considerable amount of independent variability. The amount of the observed variation is so great that in fifty or a hundred adult individuals of the same sex, collected at the same time and place, the difference of the extreme from the mean value of any organ or part is usually from one-tenth to one-fourth, sometimes as great as one-third of the mean value, with usually a perfect gradation of intervening values.

The multiplication of individuals of all species is so great and so rapid that only a small proportion of those born each year can possibly survive; hence the struggle for existence, the result of which is that, on the average, those individuals which are in any way ill-fitted for the conditions of existence die, while those better fitted live. The struggle is of varied character and intensity—either with the forces of nature, as cold, drought, storms, floods, snow, &c.; with other creatures, in order to escape being devoured, or to obtain food, whether for themselves or for their offspring; or with their own race in the competition for mates and for the means of existence; while as regards all these forms of struggle mental and social qualities are often as important as mere physical perfection, and sometimes much more important. The fact already stated, of the large amount of variability in most species, has been thought by some to show either that there can be no such severe struggle as has been suggested, or that the characters which vary so much can be of little importance to the species, and cannot therefore determine survival. But in making this objection two considerations have been overlooked. In the first place we always compare adults, and an enormous amount of destruction has already taken place during the earlier stages of life. The adults, therefore, are already a selected group. In the second place, the struggle is very largely intermittent, owing both to the occurrence only at long intervals of the most adverse meteorological conditions, while the diversity of these conditions leads in each case to the selection of a different characteristic. An exceptionally severe winter will destroy all which are deficient in one set of characters, while a long drought, or scarcity of some particular kind of food, will weed out those deficient in another set of characters. Thus, in any one year there will exist numbers of individuals which are doomed to speedy destruction under some one of the special adverse conditions which are constantly recurring; and it is this, probably, that explains why there is so much individual variation continually present, although the central or typical form remains unchanged for very long periods. This typical form is that which, under existing conditions, survives all the periodical or secular adverse changes, during which the outlying, or extreme variations of whatever kind, are sooner or later eliminated. It is for want of giving full weight to the essentially intermittent nature of the struggle for existence that so many writers fail to grasp its full significance, and continually set forth objections and difficulties which have no real importance.

We are now in a position to estimate the efficiency of Darwin's theory in explaining the wondrous and complex adaptations that abound in the organic world, as compared with that of Lamarck or of his modern supporters. And first let us take the simple case of the adaptation of fleshy and juicy fruits to be eaten by birds, causing what seems at first sight an injury to the species, but which is really most beneficial, inasmuch as it leads to the wide dispersal of the seeds, and greatly aids in the perpetuation of the plants which produce such fruits. To what possible direct action of the environment can we impute the production of fleshy or juicy pulp, with attractive colour, and with small, hard-coated seeds, in the innumerable fruits which are devoured by birds, through whose bodies the seeds pass in a state fitted for germination? There is here a combination of characters calculated to a certain end, a definite adaptation. If we suppose that in an early stage of development ancestral fruits which happened to be a little softer than others were eaten by birds, how could that circumstance increase the softness, develop juice, and produce colour in future generations of the trees or bushes that sprang from the seeds so dispersed? And if we assume that these several characteristics are positions of "organic stability," acquired through accidental variation, we have to ask why the several kinds of variation occurred together, or why neither of them occurred in the numerous species in which to be eaten by birds would be injurious instead of beneficial?

But if we begin at the same stage and apply the Darwinian theory we find that the whole process is easy of explanation. It is an observed fact that fruits vary in softness, juicyness, and colour, and seeds in the hardness or hairyness of their integuments. Any variation of primitive fruits in either of these directions would therefore be beneficial, by attracting birds to eat them and so disperse the seeds that they might reach suitable stations for development and growth. Such favourable variations would therefore be preserved, while the less favourable perished.

Now ask the same questions as to the production of the innumerable modes of dispersal of seeds by the wind, from the simple compressed form and dilated margins of many small seeds, to the winged seeds of the ash and maple, and the wonderful feathery parachute of the thistle and the dandelion. Or again, inquire as to the wonderful springed-fruits which burst so as to scatter the small seeds, as in some of the balsams; or yet again, as to the sticky glands of the sundews, and the small water-traps of the bladder-wort; and a hundred other equally strange adaptations to some purpose of use to the species, but whose development has no relation whatever to any possible direct action of the environment, though all of them are explicable as the result of the successive preservation of such variations as are known to occur, acting at various intervals, and by means of successive modifications, during the whole period of the development of the group from some remote ancestral form.

The modern advocates of Lamarckism content themselves with such simple cases as the strengthening or enlarging of organs by use, the hardening of the sole of the foot by pressure, or the enlarging of the stomach by the necessity for eating large quantities of less nutritious food. These, and many other similar modifications, may doubtless be explained by the direct action of conditions, if we admit that the change thus produced in the individual is transmitted to the offspring. That such changes are transmitted has, however, not yet been proved, and a considerable body of naturalists reject such transmission as improbable in itself, and at all events as not to be assumed without full and sufficient proof. But even if accepted it will not help us to explain the very great number of important adaptations which, like those already referred to, are quite unrelated to any direct action of the environment. Having thus cleared away some preliminary misconceptions, and stated in briefest outline the main features of the law of natural selection, we may proceed to consider the objections of those modern writers to whose works we have already referred.

Mr. Bateson's large and important volume consists mainly of an extensive collection of cases of variation of a particular kind, which have been met with throughout the whole animal kingdom, and have been recorded in all parts of the world. These are arranged systematically under nearly nine hundred numbered headings, and are in many cases well illustrated by characteristic figures. The character and morphological relations of these variations are often very fully discussed with great knowledge and acuteness, and some original views are set forth which are of interest both to morphologists and physiologists. So far as this part of the work is concerned the present writer would feel himself quite incompetent to criticise it, but would welcome it as presenting in a convenient form a great body of interesting and little-known facts. But the book goes far beyond this. The first words of the preface tell us that "This book is offered as a contribution to the study of the problem of Species;" and in a lengthy introductory and shorter concluding chapters this problem is discussed in some detail, with the view of discrediting the views held by most Darwinians; while a new theory, founded upon the facts given in the body of the work, is set forth as being a more probable one. It is therefore necessary to give some account of the nature of the facts themselves, as well as of the particular theories they are held to support.

Darwin distinguished two classes of variations, which he termed "individual differences" and "sports." The former are small but exceedingly numerous, the latter large but comparatively rare, and these last are the "discontinuous variations" of Mr. Bateson to which reference has been already made. Darwin, while always believing that individual differences played the most important part in the origin of species, did not altogether exclude sports or discontinuous variations, but he soon became convinced that these latter were quite unimportant, and that they rarely, if ever, served to originate new species; and this view is held by most of his followers. Mr. Bateson, however, seems to believe that the exact contrary is the fact, and that sports or discontinuous variations are the all-important, if not the exclusive, means by which the organic world has been modified. Such a complete change of base as to the method of organic evolution deserves, therefore, to be considered in some detail.

The difficulty which seems to have struck Mr. Bateson most, and which he declares to be of "immense significance," is, that while specific forms of life form a discontinuous series, the diverse environments on which these primarily depend shade into each other insensibly, and form a continuous series (p. 5). Further on, this objection is again urged in stronger language: "We have seen that the differences between Species are Specific, and are differences of kind, forming a discontinuous Series, while the diversities of environment to which they are subject are on the whole differences of degree, and form a continuous Series; it is therefore hard to see how the environmental differences can thus be in any sense the directing cause of Specific differences, which by the Theory of Natural Selection they should be" (p. 16). Again, at p. 69, he urges that the essential character of species is that they constitute a discontinuous series, and he asks—"Is it not then possible that the Discontinuity of Species may be a consequence and expression of the Discontinuity of Variation?" He then states, that on the received hypothesis, "Variation is continuous, and the Discontinuity of Species results from the operation of Selection." This, however, is not quite a correct statement of the received hypothesis if "discontinuous" is used in Mr. Bateson's sense, as including every change of colour which is not by minute gradation, and every change in number of repetitive parts—as of vertebræ, or of the joints of an antenna, or the rings of a worm—which is not by a gradation of the part from a minute rudiment. Such changes of colour or in the number of parts are admitted by all Darwinians as, in many cases, constituting a part of that individual variation on which modification of species depends. It is, however, on the supposed rejection of this class of variations by Darwinians that he bases what he terms "an almost fatal objection" to their theory.

Returning, however, to the supposed overwhelming importance of discontinuous variation, we pass on to the last chapter of the book, headed "Concluding Reflexions," and we read: "The first object of this work is not to set forth in the present a doctrine, or to advertise a solution of the problem of Species," and then follows immediately a further discussion of this very theory of discontinuity, which *is* set forth as a doctrine, and as a help to the solution of that problem. We are told that the difficulties of the accepted view "have oppressed all who have thought upon these matters for themselves, and they have caused some anxiety even to the faithful"; it is urged that "the Discontinuity of which Species is an expression has its origin not in the environment, nor in any phenomenon of Adaptation, but in the intrinsic nature of organisms themselves, manifested in the original Discontinuity of Variation"; that, "the existence of sudden and discontinuous Variation, that is to say, of new forms having from their first beginning more or less of the kind of *perfection* that we associate with normality, is a fact that disposes, once and for all, of the attempt to interpret all perfection and definiteness of form as the work of Selection." And then comes the positive statement—"The existence of Discontinuity in Variation is therefore a final proof that the accepted hypothesis is inadequate" (p. 568), and after several more pages of illustration and argument, the final conclusion is reached that—"it is quite certain that the distinctness and Discontinuity of many characters is in some unknown way a part of their nature, and is not directly dependent upon Natural Selection at all."

Before going further it will be well to make a few observations on these very definite and positive conclusions at which Mr. Bateson has arrived; and it must be remembered that this volume deals only with one portion of the subject even of discontinuous variation, which is itself, if we exclude monstrosities, only a small fragment of the whole subject of variation. The impression that will be produced on those who have given special attention to the relations of living organisms to each other and to their inorganic environment, will be that of an academic discussion, dealing to a large extent with words rather than with the actual facts of nature. The author's main point, that species form a discontinuous series, and that specific differences cannot therefore have been produced by any action of the environment, because that environment is continuous—an argument which, as we have seen, he dwells upon and reiterates with emphasis and persistency—rests wholly upon the obvious fallacies that in each single locality the environment of every species found there is the same, and that all change of environment, whether in space or time, is continuous. To take this latter point first, nothing can be more abrupt than the change often due to diversity of soil, a sharp line dividing a pine or heather-clad moor from calcareous hills; or to differences of level, as from a marshy plain to dry uplands; or, for aquatic animals, from the open sea to an estuary, or from a non-tidal stream to an isolated pond. And when, in the course of geological time, an island is separated from a continent, or volcanic outbursts build up oceanic islands, the immigrants which reach such islands undergo a change of environment which is in a high degree discontinuous.

Even more important, perhaps, is the fact that, everywhere, the environment as a whole is made up of an unlimited number of sub-environments, each of which alone, or nearly alone, affects a single species, as familiarly included in the term, "their conditions of existence." The mole and the hedgehog may live together in the same general environment, yet their actual environments are very different owing to their different kinds of food, habits, and enemies. The same thing applies to the rabbit and the hare, the rook and the crow, the ring-snake and the viper; and still more when we look at animals of greater diversity, as the otter and the badger, the dung-beetle and the cockchafer, and a hundred others that might be quoted. Now, though all these creatures may be found together in the same area, each of them has its own "environment," to which it must be adapted in order to maintain its existence. Many species, however, live, as it were, on the borders of two distinct environments, as when they obtain different kinds of food at different periods, being then exposed to different enemies and varied climatic effects. In such cases, it is easy to see that a small modification of structure might enable them advantageously to change their habits, and thus obtain what would be practically a different environment. This is well seen in those closely allied species which have somewhat different modes of life—as the meadow pipit (*Anthus pratensis*) and the tree pipit (*Anthus arboreus*)—the former having a long, nearly straight claw to the hind toe, a more slender bill, and a rather greener tinge of colouring, all modifications suited to its different habits and distinct physical surroundings. Here we have an example in nature of how environments, even when continuous as a whole, may become quite discontinuous in relation to two species differing in very slight characters. Darwin dwelt much upon this phenomenon, of new species being formed when any body of individuals seized upon vacant places in the economy of nature, and by means of comparatively slight variations became adapted to it. It is what we see everywhere in the world around us.

It thus appears that what is evidently supposed to be a very powerful argument leading to the conclusion that discontinuous variations as a class are those which are of vital, if not exclusive importance in the production of new species, entirely breaks down when confronted with the facts of nature. It does not, however, follow that, because an unsound *à priori* argument has been used to call attention to these variations, and because they have been set before the world in a way to suggest that their importance in relation to the origin of species is a new discovery calculated to revolutionise the study of this branch of biology, they are, therefore, of no value in this connection. We will, therefore, now proceed to consider them on their own merits as possible factors in the process of organic evolution. For this purpose we must briefly indicate the nature of the variations so laboriously recorded in this volume.

These consist of what are termed meristic variations, that is, variations in the number or position of parts which occur in series, whether linear, bilateral, or radial. Such are the variation in the number of segments of annulosa and arthropoda, such as worms, leeches, centipedes, &c.; in the antennæ and legs of insects; in the vertebræ, ribs, teeth, nipples, limbs, and toes of vertebrates; in the rays of starfish, encrinites, and allied animals. The ocelli and other symmetrical markings on the wings of butterflies are also recorded, as well as numerous malformations when these affect serial or symmetrical organs.

On carefully looking through the cases of variation in this volume we are struck with the large proportion of them which exhibit more or less deformation or want of symmetry, culminating in the various kinds of monstrosity. In Chapter III., on the variations of vertebræ and ribs, we find vertebræ imperfectly divided in snakes and frogs. Numerous cases of abnormalities in human vertebræ are given, usually exhibiting asymmetry or deformation, and similar variations are found in the anthropoid apes, but here there is apparently more of regularity and symmetry. The greatest amount of this kind of variation occurs in the sloths, as might be expected when we consider that they are the most abnormal of mammals as regards the cervical vertebræ. In Chapter VIII. numerous cases of supernumerary mammæ are recorded, almost all of which are unsymmetrical. The variations in the number or form of the horns in sheep, goats, and deer recorded in Chapter XI. show them to be usually more or less irregular.

Nearly a hundred pages are devoted to the digits (fingers and toes) of mammals and birds, about one hundred and forty cases of variation being recorded. Almost the whole of these present, more or less, want of symmetry, while a large proportion, as the double-handed and double-footed children, and the six or seven-toed cats, can only be classed as monstrosities.

In succeeding chapters the variations in the antennæ and leg-joints of insects; in the radial parts of medusæ and encrinites; in the medial structures of fish, insects, molluscs, &c., which become sometimes double; in the eyes and colouration of flatfish; in duplicate or branching legs of insects and crustaceans; in extra limbs of batrachia; and, lastly, double monsters, are all discussed at great length, and are illustrated by a number of very interesting wood-cuts. But almost the whole of these can only be classed as malformations or monstrosities which are entirely without any direct bearing on the problem of the "origin of species."

Nothing can better show the small value of the book from this, which is the author's own, point of view, than the large amount of space devoted to the various monstrosities of the hands and feet of man and of some of the mammalia. Not only throughout all mammals, but also in the case of birds, reptiles, and amphibia, five is the maximum number of the toes or fingers. These may vary in size or in proportions, they may be reduced in number by coalescence, or by the loss of the lateral digits; they may be strangely modified in form and function, as in the flappers of the whale, or in the wing of the bat, yet never once in the whole long series of land-vertebrates do they exceed five in number. Yet we have six, seven, or eight-fingered, double-handed, or double-footed children; similar malformations in monkeys; six and seven-toed cats; four, five, or six-toed pigs; double-footed birds, and other monstrosities, described at great length, and all their peculiarities discussed in the most minute detail and from various points of view, in a work presented to us as "a contribution to the study of the problem of species." Many of these malformations have been observed among animals in a state of nature, and in fact, Mr. Bateson believes that they occur as frequently among wild as among domesticated animals. Considering how rarely the former cases can be observed, they must be everywhere occurring; yet in no one single instance do they seem to have established themselves as a race or local variety on however small a scale. Yet we know that in the case of the six-toed cats, and probably in other cases, they are easily transmissible; and we must, therefore, conclude that all these irregularities and monstrosities are in a high degree disadvantageous, since when subject to free competition with the normal form in a state of nature they *never* survive, even for a few generations.

As the volume we are discussing is entirely devoted to variations in the number or position of the serial parts of organisms in relation to the origin of species, it becomes necessary to lay some stress upon the very familiar, but apparently overlooked fact, that, among all the higher types of life at all events, the most stable of all characters, and the most permanent during long periods of evolution, and throughout changes which have led to the production of a marvellous variety and abundance of specific forms, are these very characters of the *number* and relative positions of serial organs; whence it follows that variations of this kind can only have led to specific changes at enormously long intervals, and that, as a general rule, they can have had nothing whatever to do with the origin of an overwhelming majority of living species.

First, we have the four limbs of vertebrates, which among all the marvellous variety of form and function, on land, in the water, or in the air, is never exceeded, and appears to have been fixed at a very early stage of the development of the vertebrate type. Equally fixed, and extending through a still vaster range of modifications of specific forms, are the six legs and four wings of true insects, which, as in vertebrates, may be reduced but never increased in number. Still more extraordinary, because less obviously connected with the main structure and functions of the organism, is the limitation and permanence in the number of the subdivisions of limbs and other appendages. There is no obvious reason why in land-vertebrates the divisions of the hand and foot should never exceed five, yet, not only is this number the maximum, but it may be considered the normal number of which all others are reductions, since it still prevails largely in the marsupials, rodents, carnivores, primates, and lizards; and the five-toed land-vertebrates (excluding birds) are probably far more numerous than those with a lesser number.

In birds there are only four toes as a maximum, and comparatively few have a smaller number. But we have here a peculiarity in the numbers of the toe-joints which does not occur in any other vertebrates. These form a series in arithmetical progression, the hind toe having two, and the others three, four, and five joints in regular order; and this rule is very nearly universal, the only exceptions being in some of the swifts and goatsuckers, whose habits render the feet of comparatively little importance, while their general organisation is of a somewhat low type.

Coming to insects, we again find the legs consisting of a limited number of parts, and, strangely enough, this number is again five—the coxa, trochanter, femur, tibia, and tarsus. The tarsus, however, is subdivided into small movable joints, and these, too, are five as a maximum, but in certain groups are reduced to four, three, or two. The five-jointed tarsus is, however, the most prevalent; and in the enormous order of coleoptera or beetles, comprising at least one hundred thousand described species, fully half belong to families which have the tarsi five-jointed. Even the antennæ, although they vary greatly in the number of joints, yet in numerous large groups comprising many thousands of species, they have the number of joints constant. Another indication of the tendency of serial parts to become fixed in number, is the typical limitation of the cervical or neck vertebræ of mammalia to seven joints. This number is wonderfully constant, being the same in the long necks of the giraffe and camel, and the very short necks of the hippopotamus, porpoise, and mole, the only exceptions in the whole class being some of the sloths, which have from six to ten, often varying in the same species, and the manatee, which has six.

Now, if we consider the enormous extent of these fixed numerical relations of important parts of the organism in the higher vertebrates and in insects, both as regards the number of living species affected—perhaps ninety-nine per cent. of the whole—and as regards their range in time, throughout the whole of the tertiary and secondary, and even a considerable portion of the palæozoic periods—and if we take account of the vast number of extinct species, genera, and families needful to complete the various lines of descent from the earliest known forms, presenting the same numerical relations to those now living—we shall be able to form some conception, however inadequate, of the overwhelming frequency and importance of variations in the size, form, proportions, and structure of the various parts and organs of the higher animals, as compared with variations in their number. No doubt, in the earlier stages of organic development, numerical variations were more frequent and more important, as they are now among the lower forms of life; but at a very early period in geological history, the main numerical relations of the essential parts of the higher organisms became more or less fixed and stable, and have in many cases remained unchanged through a large proportion of the period comprised in the geological record. The four limbs of vertebrates were already established in the fishes of the Devonian period, as were the four wings and six legs of true insects in the cockroaches and archaic orthoptera of the Carboniferous; and almost all subsequent changes have resulted from modifications of these early types. The earliest mammals of which we have sufficient knowledge have the typical five-toed feet, and the earliest birds appear to have had the same progressive series of toe-joints as now prevails.

We are thus irresistibly led to the conclusion that, among all the possible forms of variation now occurring, those affecting the *number* of important serial parts among higher organisms, are those which have the least possible relation to whatever modification of species may *now* be going on around us, or which has been going on during a large portion of geological time. Yet it is to variations of this nature, a large proportion of which are mere malformations or monstrosities, that the bulky and learned volume we are discussing has been devoted. The author of this book puts forward these malformations and irregularities, mixed up with a proportion of normal variations, under the misleading name of "Discontinuous Variations," as if they were something new, and had been ignorantly overlooked by Darwin and his followers; and he loses no opportunity of telling us how important he thinks they are, what difficulties they enable us to overcome, and how they are the beginnings of the establishment of a sure base for the attack on the problems of evolution. In so doing he has entirely failed to grasp the essential features which characterise at least ninety-nine per cent. of existing species, which are, slight differences from their allies in size, form, proportions, or colour of the various parts or organs, with corresponding differences of function and habits, combined with a wonderful amount of stability in the numerical relations of serial parts, extending sometimes only to genera, but more usually to families, tribes, orders, or even to whole classes of the higher animals. It is differences of the former kind that do actually characterise the great majority of species;[1] they affect those organs which vary most frequently and most conspicuously in the individuals of every fresh generation; and they constitute that individual variation on which Darwin always relied as the essential foundation of natural selection, and which his followers have shown to be far more abundant and of far greater amount than he was aware of; and, lastly, they afford amply sufficient material for the continuous production of new forms. Rarely

(1) Mr. Bateson, however, makes the extraordinary statement that "it is especially by differences of number and by qualitative differences that species are commonly distinguished" (p. 573). Species-makers know too well that, among the higher animals at all events, it is not so!

in the history of scientific progress has so large a claim been made, and been presented to the world with so much confidence in its being an epoch-making discovery, as Mr. Bateson's idea of discontinuous variation corresponding to and explaining the discontinuity of species: yet more rarely has the alleged discovery been supported by facts which, though interesting in themselves, are for the most part quite outside the general conditions of the complex problem to be solved, and are therefore entirely worthless as an aid to its solution.

Before leaving this part of the subject we may note the extension of definite numerical relations to plants as well as to animals. In dicotyledons we have a typical five-petalled flower or a corolla with five divisions, a character which prevails in irregular as well as in regular flowers, and often when the stamens are not a multiple of five, as in mallows, bignonias, and many others. Some form of five-parted flower prevails throughout many extensive natural orders, and comprises probably a considerable majority of all dicotyledonous plants. A three or six-parted flower is almost equally a characteristic of monocotyledons, prevailing even among the highly specialised and fantastically formed Orchideæ and Irideæ, thus again demonstrating how large a portion of the specific modifications of organisms are independent of variations in *number*, but depend wholly upon variations in the size, form, colour, and structure of the various parts and organs.

Other matters of importance in Mr. Bateson's work, together with some theories recently advanced by Mr. Francis Galton, will be discussed in the concluding portion of this article.

ALFRED R. WALLACE.

Reprinted from "NATURAL SCIENCE," Vol. X., No. 59, January, 1897.

15

The Position of Morphology in Zoological Science.

BY

E. W. MacBRIDE, B.A., B.Sc.,

Fellow of St. John's College, Cambridge.

The Position of Morphology in Zoological Science.[1]

A PAPER which proposed to insist on the cardinal value of morphology in the science of zoology, would have been held some years ago to be an entirely superfluous statement of a universally recognised truth. It cannot, however, be denied that there has been growing up amongst zoologists in the past ten years a feeling of dissatisfaction with morphological methods, and a tendency to disparage altogether morphology as a means of research. This feeling finds expression, for instance, in Ray Lankester's article on Zoology in the "Encyclopædia Britannica," where we read that "pure morphography has long since ceased to be a principal line of research," and that the attention of young students should not be confined to "what are now, comparatively speaking, the less productive lines of research." In Bateson's "Materials for the Study of Variation" we meet the broad statement that the morphological method has failed. Driesch and others who work on the same lines estimate the value of morphology at a very low figure.

I propose in the present essay to examine briefly the rival methods which have been put forward as demanding chief attention from zoologists, and shall show that all of them, valuable as they undoubtedly are, suffer from defects from which morphology is free. I shall further inquire to what causes the feeling of discontent with morphological methods is due, and finally I shall tentatively indicate certain ways of dealing with morphological facts which seem to me likely to be free from the objections which have been raised to other methods, and promise to throw fresh light on the general problems of zoology.

The lines of research which have been put forward as being more important than morphological investigations and comparisons, are mainly three, viz., Experimental Embryology, Study of Individual Variations, and Statistical Studies in Variation, or Mathematical Zoology. All are avowedly attempts to solve one of the chief problems of zoology, viz., the nature and causes of animal change or variation. Experimental embryology founded by Roux and carried on with such success by Driesch, Hertwig, and Loeb, has for its aim the isolation of the various processes the conjoint working of which con-

[1] Paper read before Section D of the British Association, September 22, 1896.

stitutes ontogeny. It is therefore to be looked on as a new kind of dissection. Many embryologists have attributed to the visible units observed in a segmenting egg, independence of growth and a definite function in building up the organism. The experimental embryologist, however, by forcing these units into abnormal positions, or by isolating them, is able to demonstrate that such attributes are impossible, and that the real factors into which development is separable are not identical with the visible differentiation which the germ exhibits. Driesch distinctly states that this dissection is the whole aim of experimental embryology, but some of his followers seem to imagine that by such means it is possible to discover the ultimate causes which bring about variation. This idea is, I think, a totally mistaken one. No examination of the changes which, by the application of physical or chemical means, we are enabled to bring about in the outer structure of the organism, will bring us one step nearer the discovery of those causes which are able to modify its inner hereditary potentiality. We may, like Driesch, force that part of the egg which normally produces the head to give rise to the tail, or, like Herbst, turn endoderm into ectoderm; all we arrive at is a resultant of the combined working of hereditary tendency and effect of environment.

The study of individual variations stands on a different basis. The modifications which species undergo are *ex hypothesi* made up of a summary of individual variations, and it seems quite proper to begin with a consideration of these; but at the outset we are met with a most serious difficulty. We have no means of distinguishing modifications, which have been produced by the action of environment on the particular individual we examine, from those due to variations in its hereditary qualities. Still further, the individual variations which appear most prominent to us are often those which there is strong reason to believe have never taken part in the evolution of species. In his "Materials for the Study of Variation," Mr. Bateson has collected numerous instances of supernumerary digits in Vertebrata and of branched legs among the Insecta; yet, in all the hundreds of species of Mammalia, and the hundreds of thousands of species of Insecta, no solitary instance is known where a variation of this kind has become the distinguishing mark of a species. Even of those changes due to variation in the hereditary powers, it is clear that only a small proportion concern us. For, in order to become a real factor in evolution, it is necessary that a variation should not only be transmissible to the offspring, but further, that it should occur sufficiently frequently to give natural selection an opportunity of taking advantage of it.

The Statistical Study of Variations, which we owe to Dr. Galton and Professor Weldon, cannot, I think, be assailed on theoretical grounds. This method aims at representing in a curve, not only the extent of variation in a given character met with in a species, but also the number of individuals exhibiting any particular variation. We can thus see at a glance the proportion between the average and the departures from it, and if we should find, by comparing curves constructed from the examination of individuals of different ages, that the death-rates of the possessors of different variations were different, we should have reasonable ground for supposing that natural selection was weeding out certain variations. We should further have an answer to the question whether the species was being modified or not—this answer being positive or negative according as the death-rate was greater on one side of the average than on the other, or equal on both sides.

The main objections which can be urged against this method are of a practical nature. First, we isolate a character, and try to determine whether or no its possessor suffers by its presence. But "characters" are mere mental conceptions, they do not exist by themselves, and natural selection acts, so to speak, on the balance of all the characters. Of course, if we could prove that individuals possessing a certain character had a lower death-rate than individuals without it, we might expect that that character would become a distinguishing feature of the species, though the survival of those that possessed it might not be due to its utility, but to some constitutional peculiarity of which it was the by-product. How are we to determine such an association of death-rate and variation? The attempt has been made by drawing a curve for the same character in the case of young and of older animals. The curve was flatter in the case of the younger animals; that is, the number of deviations from the mean was found to be greater in them: hence it is assumed that these abnormal forms are continually being weeded out. It is possible, however, that there may be a self-regulating tendency in growth. Are not abnormalities observed in children often toned down in later years?

There is another objection, the validity of which would not be admitted by many, but which seems to me to have a certain weight, and that is this: So far as we can discover, the condition of the organic world has remained relatively stable during the historical epoch, and no new species are known to have been formed. It is a question, therefore, on the one hand whether the conditions which brought about the great variability of which we see evidence in the geological record, still persist, and if not, whether the process of evolution be not so slow, that the infinitesimal period over which our observations can extend gives us no clue as to its direction.

From the standpoint of morphology it seems to me that we are free from all these difficulties. We take as our units not individuals but species, and if the doctrine of descent be admitted, we must infer that specific characters have themselves been of importance in the struggle for existence, or have been inextricably bound to others which have. If specific characters then are our material, certainly they offer a sufficiently wide field to work on and give us a unit small enough to start with, since there are many specific distinctions far less obvious than many individual variations. Many specific characters are doubtless merely associated with other characters which really determine the survival of their possessors, but this is true to a less degree of generic characters, and as we pass over to family and ordinal groups we get on safer and safer ground in assuming that we are dealing with features directly due to natural selection.

Why then has this feeling of dissatisfaction with the method of morphology grown up? The main reason is, I think, a conviction that it proves too much. The most discordant views as to the relationship of animals and their ancestry have been drawn from the same facts, and there does not seem to be any court of appeal before which rival views can be brought. Then again, continued study has forced home the conviction, that the processes of evolution are much more complex than was at first imagined, and that so far from being a simple process from the less to the more differentiated, the converse, viz., *degeneration* or simplification of structure, is also going on; further, that similar structures are sometimes independently developed along different lines of descent, in virtue of what was called "parallel" or "convergent evolution," but termed by Professor Lankester *homoplasy*. Now the discovery of the great principles of degeneracy and homoplasy, whilst it explained many points, has caused considerable doubt as to the certainty of morphological reasoning. For really, when armed with the principle of progressive degeneracy as well as with that of progressive differentiation, there is no limit to the powers of the evolutionary theorist; one can derive literally any one animal from any other by first deleting all the obnoxious organs in the supposed ancestor, and then evolving any number of new ones. Then again, if similar structures may have been developed independently in two different stocks by the action of similar external conditions, where is one to draw the line? How far is one justified in relying on similarity in structure as a criterion of community of descent at all? These, I think, are some of the questions which have underlain the feeling of scepticism as to the value of morphology which has crept over many zoologists, and which have caused, I confess, much trouble and distrust in my own mind. I now venture to suggest ways of looking at morphological facts, which seem to me more fruitful than the ordinary methods, and which have given me fresh hope in the pursuit of morphological study.

First, it is a mistake to assume that in tracing a supposed line of descent we are at liberty to assume that any conceivable variation may have occurred, variations, for instance, the utility of which we are not bound to explain. I think if we take specific and generic distinctions as our units, we are bound to show that some parallel change to the one we postulate has in all probability taken place. Thus there has been an immense amount of discussion as to how the pentadactyle limb was derived from the fin of a fish; but no one, so far as I am aware, has examined with care the cases of those Teleostean fish, like some species of blenny, which come out of the water and seek prey between tide-marks, where a fin has been to some extent transformed into a supporting limb. I do not wish to dogmatise against the possibility of changes having taken place in past time altogether different in kind to those of which we find evidence in present specific differences; but I do maintain that if we assume such changes in explaining the present structures of animals we are on utterly unsafe ground. My suggestion then is that by carefully comparing and tabulating specific and even generic differences we may be able by induction to arrive at "laws of successful variation." An example or two will serve to make clear what I mean. If we review the group of the Lamellibranchiata, we are struck by such forms as *Teredo* and *Pecten*. *A priori* it is possible to argue that the idea that these were derived from the ordinary type of Mollusca is hypothetical. Practically all zoologists are agreed about it, no different explanation having so far as I know ever been suggested. Now my point is that cases like these give us definite data to go on; they really enable us to ascertain now,—what Bateson has looked forward to doing only in the remote future—that certain changes are possible to certain animals. Perhaps it may be retorted that all this is known and acted on. My reply is that many changes have been postulated, which have no analogue amongst variations that we know must have occurred. Balfour postulated the formation of a new mouth; Dohrn that of a new arm. All through the Mollusca we find no such fundamental change, nor the foundation of any new type of skeleton such as the supporters of the Annelid theory are bound to postulate.

If we now turn to the difficulty of distinguishing primitive and undifferentiated from degenerated structures, we shall find, I think, that objections may be made to the current modes of reasoning on this subject. It is often implicitly assumed (1) that if an animal can be shown to be degenerate in one respect, it is not primitive at all, and throws no light on the ancestry of a group; (2) that any amount of degeneracy may be followed in the history of the race by any amount of forward evolution. I shall give reasons for questioning both suppositions. To prove that the first is a real factor in theorising, we have only to remember the war waged round *Amphioxus*. Few would deny that it is degenerate in some points; the question at issue is, Does it in its general organisation represent the ancestor of Vertebrata or not? Now it seems to me that on *à priori* grounds we have every reason to expect that all animals, which possess on the whole a primitive organisation will be degenerate in some features. For their modified relatives which have departed from the ancestral type have *ex hypothesi* been forced to do so by natural selection, and how have these primitive animals been able to escape from that pressure of environment which modified allied forms? In some cases, perhaps, isolation on oceanic islands, or in small lakes may have allowed them to do so; but in the case of what we may term phylum-ancestors such as *Amphioxus* and *Peripatus* such explanations are futile. The grade of structure they present, dates from such a remote epoch that no physical barrier will have remained constant in the interval, added to which their wide distribution at once negatives such an idea. No; the general method in which such animals escaped from the stress of environment, was by taking to burrowing or sessile modes of life, and this has inevitably carried a certain amount of degeneracy with it. The idea that active vigorous vertebrates are descended fnom a sluggish mud-eating worm like *Balanoglossus* must strike many people as highly improbable, but that *Balanoglossus* is descended from a free swimming form with well developed eyes we know from the structure of its larva to be extremely probable, and there is nothing violent in the supposition that this same form may have given rise to the Vertebrata. I think, if once the dictum, "All primitive animals are also in some degree degenerate" were accepted, a harmonious explanation of many discordant facts would be attained.

In this connection I may say that such phrases as "degree of modification" are in need of definition. I think many zoologists have admitted there are two kinds of modification at work: first, in the intensity of metabolism or the degree of vitality, by which we mean the degree of specialisation of the organs for carrying on the vital processes—digestion, respiration, circulation, excretion, &c.; and secondly, in shape and form of the outer appendages, or of the general shape of animals. Now, it is the first kind of modification to which zoologists attach weight. What we desire above all to know is how the complicated physiological mechanisms represented by the higher vertebrates have been built up. It is assumed that variations in form and size—the outgrowth of flaps and lobes, &c.—are things which may have been accomplished in a comparatively short time. When, therefore, zoologists speak of animals being primitive, they mean with regard to internal organisation. On grounds of the relatively greater importance of the latter, they separate the beaver and wombat, the great ant-eater and the pangolin, &c., &c. This distinction between internal and external structures is sometimes explained by saying that the latter are adaptive, as if all characters were not ultimately adaptive. Explicitly stated, the belief underlying such principles of classification is: Improvement and elaboration of internal structure and constitution is a slow process; modification of external structure is a rapid one, and has given similar results again and again. The Brachiopoda are a good instance of a group where the external form is highly specialised, but where inner differentiation is at a very low ebb. They exhibit a most primitive condition of the excretory, generative, circulatory, and nervous organs. These animals form a part of the oldest fauna known to us; but if the view which I have been trying to propound is correct, the conclusion that the date of the appearance of this fauna is enormously removed from the beginning of life, because it contains highly specialised forms, must be taken with considerable abatement.

Turning now to the question whether we can legitimately assume that degeneracy and differentiation have alternated in the history of a species—in a word, whether degenerate ancestors have given rise to active forms with highly developed sense-organs—let us glance at those cases where all will admit that a certain amount of recovery has occurred. One of the best-known cases is that of *Pecten*. There is strong reason for believing that all lamellibranchs are descended from more active forms provided with cephalic eyes and tentacles, and separate cerebral and pleural ganglia. Owing to their sluggish, burrowing mode of life, and gross non-selective feeding, these features have been lost. The oysters, to which *Pecten* is not distantly allied, have carried this degeneracy to its extreme point—the foot, one adductor muscle, and the pedal ganglia being likewise absent. *Pecten* has recovered the free-swimming life, and has developed a new set of sense-organs; but none of the lost structures have been recovered. I know of no other case where it is at all probable that recovery has taken place, and there is no ground for assuming that burrowing forms could ever give rise to active descendants. This brings us to the question, how primitive or undifferentiate can be distinguished from degenerate features. How are we to say, for instance, what features in *Amphioxus* we may regard as ancestral, and what as secondary; or in *Peripatus* or *Chiton*? I do not assert that any absolute criteria can be put forward; each case must be judged on its merits: but certain suggestions can be made. The criterion of primitive characters is their synthetic character—that is, they serve to link together different groups. Why are the gill and foot of *Nucula* said to be of a primitive character? Because they agree, in contradistinction to those of the lamellibranchs, with the gastropod gill and foot. An organ may be said also to be primitive if it combines functions distributed in other animals amongst different sets of organs. Thus, the cœlom of brachiopods combines the functions of excretory organ, generative organ, and body-cavity: so we regard it as being in a very primitive condition. Underlying such reasoning there is a principle I believe to be sound; it is that new organs are never developed from functionless rudiments—as Darwin at one time thought himself forced to believe—but arise by modification of pre-existing organs. Where the function of an organ is changed, the newer function must have existed with, but subsidiary to, the old one. Eyes and ears would thus be local spots of peculiar sensitiveness on a skin which responded to both light and sound. Degenerate organs are no doubt simplified, but not only are they not synthetic in the sense mentioned above, that they do not recall the conditions of affairs in other groups, but they are not correlated with the state of development of other organs. A good instance is found in the limbs of perennibranchiate Urodela. These are, it is true, constructed on the pentadactyle plan, but they are exceedingly feeble, and the number of digits is in almost every case reduced. They are thus unable to support the weight of the body, the purpose for which the pentadactyle limb was originally evolved, nor do they, on the other hand, show any of the characters of fins. Hence, we conclude that perennibranchiates have been derived from caducibranchiate forms—forms, at any rate, which walked more and swam less,—and the life-histories of *Siredon* and *Menobranchus* have now proved that we are right. Then, again, in the case of the head of *Amphioxus* we notice that it is asymmetrical, and that the brain and sense-organs are almost entirely obsolete. But we know that the whole organisation of Vertebrata is permeated by bilateral symmetry, and that they all have well-developed brains and sense-organs, and lead typically a free, roving life. To this life only can we attribute the fact that *Amphioxus*, like other vertebrates, is flattened in a vertical plane, since only in swimming could a body of such a shape be easily maintained in equilibrium; asymmetry and feeble sense-organs are inconsistent with such a life, and hence we interpret them as secondary features, due to the secondarily-acquired burrowing habits.

One of the most vexed questions in zoology has been the value of the evidence afforded by embryology. The older anatomists roundly asserted that the ontogeny of the individual was a recapitulation of the phylogeny of the race. They endeavoured to find ancestral meanings for all the embryonic structures which they had observed. Lately it has become fashionable to look coldly on such theorising, and some have even gone so far as to deny that there is any evidence that ontogeny is in any sense a repetition at all. I cannot but think that the latter class of zoologists are in much the same position as the theological opponents of the doctrine of evolution —they are most imperfectly acquainted with the facts. It must be remembered that comparative embryology is only an extension of comparative anatomy; that it is most arbitrary to say that only sexually adult forms are to be compared with one another; and that the conclusion that resemblance between the immature stage of one animal and the mature stage of another is indicative of affinity, is precisely on all fours with a similar conclusion drawn from a comparison with one another of two adult stages. But there are many cases where no one really doubts that the affinity indicated by ontogeny is correct; in other words, that in these particular cases ontogeny is a repetition of past history. Such cases are the pentacrinoid young of *Antedon*, with the conspicuous basals and orals, the cyclops-like larva of the parasitic copepods, the tadpole-like larva of the ascidians, and, in general features, the tadpole of the frog. Now, if there be this undeniable hereditary basis for ontogeny in some cases, it is exceedingly unlikely that it is a factor which is only sporadically present. The process of development of all animals from the egg is in all probability fundamentally the same kind of process in all cases, and made up of the same factors, though some may be more prominent in some cases than in others.

Of course, everyone admits that there are numerous features in ontogeny which are not due to ancestral repetition, but to subsequent modification of the larva, and the question is how are the results, due to these two factors, to be distinguished from one another. Now, an important step towards attaining this result has been made by Mr. Sedgwick in his theory of the relation to each other of the embryonic and larval types of development. This theory is briefly as follows: An embryonic stage of development is nothing but a larval stage, which has been sheltered from the external world, by either being enclosed in an egg-shell or retained in the body of the mother, and modified in consequence. The larva retains ancestral features, because it is subjected to ancestral conditions of life; when, however, as in the case of reptile ontogeny, it has become converted into the embryonic type, then a change, such as the loss of limbs, when it occurs, can affect the development as a whole, and not even embryonic vestiges remain, as is the case with snakes. On the other hand, so long as the larva of the frog lives in water, it must retain many fish-like features. I think, however, we should make a mistake if we limited the influences tending to retain ancestral structure to the outer conditions, when these latter happen to be of an ancestral type. It is to me impossible to suppose that the general form of insect larvæ, the vermiform shape, and the large number of almost similar segments, is not an ancestral feature; but in view of the extraordinarily diversified habits of these larvæ, we cannot suppose that the influence of outer conditions has retained it. If, however, we say that the larval form is the combined result of outer and inner conditions, we shall, I think, be nearer the truth. By inner conditions I mean the intensity of the metabolism of an animal, correlated with which is the differentiation from one another of the organs fulfilling the various functions; such a level of metabolism as the adult possesses being only gradually obtained, when the said level is a comparatively high one. Thus, when the long and comparatively undifferentiated nervous system of the caterpillar becomes converted into the concentrated nervous ganglia of the butterfly, there is no doubt that we have reached a higher level of life.

Suppose, then, that the ancestral features of ontogeny are due to the repetition of ancestral outer and inner conditions, we can make a rough estimate of characters which will *not* tend to be preserved by these causes, but which, for the most part, will be obliterated by subsequent modification. Chief among these is *size*: most larvæ are comparatively minute; only in a few cases does the larval stage rival in size the adult, while in very few cases (urodele amphibians) it tends even to supplant it. Now, along with reduction in size goes, in all probability, reduction in number of a series of homologous organs performing the same kind of function, since there is little doubt that the repetition of members is a phenomenon of fundamentally the same nature as vegetative reproduction, and that it is, primarily at any rate, correlated with growth in size. Thus, we can understand why the nauplius larva should lose the long series of post-oral parapodia-like appendages which we have reason to believe the annelid ancestor of arthropods possessed, and should retain only those first three modified ones, the modification of which was probably one of the chief changes by which an annelid was converted into an arthropod. A most interesting confirmation of this view is obtained by comparing the nauplii of the various crustacean groups. The most annelid-like order is that of the phyllopod Branchipoda, and here the nauplius still retains traces of the post-oral segmentation. In the other groups, notably the cirripedes and the ostracods, the nauplius has lost all traces of this segmentation, and is obviously secondarily modified, since in each case it shows precociously some features of the adult.

The general result of this way of regarding ontogeny will be that we shall regard no larva as purely secondary in all its features, and that where we compare two animals more or less allied, we shall attach the greatest importance to the ontogeny of that one which has the longest larval history. It is, so far as I know, a rule without any exception that when we compare corresponding stages, what is obscure and difficult to interpret in the embryo, becomes clear and instructive in the larva. The Echinodermata have perhaps the longest larval history in the animal kingdom; they begin free life as blastulæ, and in no group is the process of the formation of the primary germinal layers so diagrammatically clear.

Finally, we have to consider the greatest difficulty of all those involved in morphological reasoning, namely, that which the recognition of the principle of homoplasy brings with it. The proposition that similar organs might arise in different animals under the stress of similar conditions, seemed at first to offer merely a convenient solution of some difficult problems, so long as the organs in question belonged to members of widely different families, such as the tracheæ of insects and arachnids for example. It is, however, becoming every day clearer, that such parallel evolution has taken place again and again within narrow circles of affinity. Let any morphologist examine the structure of a large group; let him by careful comparison of the various species with one another, arrive at an idea of the primitive form from which all were derived, and then let him attempt to indicate the lines along which the different forms have been evolved. He will find himself driven to the conclusion that important structural features on which he would be naturally inclined to found his system of classification, have been developed twice or thrice. Numberless instances of this might be given. Calcareous sponges used to be divided into three well-marked classes, according to the character of their canal system, viz :—the ascons, the sycons, and the leucons, forming three stages in an ascending scale of differentiation. Now Sollas and other competent spongiologists consider that the leucon type has been evolved many times amongst the different families into which the sycons are divided. The horny sponges and the sponges devoid of spicules have likewise had in each case two or three roots. Among the echinoderms we meet with similar cases on every hand. One of Perrier's main divisions of the asterids is that of the Valvata, in which the plates which form the skeleton are covered with a uniform granular coating, there being practically no spines. This division includes long-armed and short-armed forms; the latter glide by insensible gradations into the short-armed forms of the group Paxillosa, in which the armature is composed of circles of spinelets borne on a button, of which *Astropecten* is the best known example. The long-armed forms probably have no affinity with Paxillosa. The term "short-armed" is not quite correct; it is not only that the radii are comparatively short, but that the arms have coalesced with each other laterally. Amongst the ophiurids, the habit of carrying the young in the genital bursæ, which gives rise to great differences in the development, has been independently acquired in four or five distinct genera, other species of which give rise to free-swimming larvæ. Among echinids the eccentric position of the anus, and the peculiar modification of the ambulacra, involved in their assuming the petaloid form, when the tube-feet become broad respiratory leaves, is found in the Clypeastridæ and Spatangidæ. As the first group retain the jaws of the regular echinids whilst the second have lost them, one might at first sight infer that the spatangids were merely a further development of the clypeastroid type, but this supposition is precluded by the fact that in both groups we find fossil forms with perfectly normal ambulacra and almost central anus. Among the annelids, the group of the tubicolous annelids is now divided up into families which are placed with families of the Errantia. Amongst arthropods, those air-breathing arachnids which retain lung-books, the Pedipalpi on the one hand and the scorpions and spiders on the other, have, according to Laurie,[1] been derived from the water-breathing eurypterids along two distinct lines. The land-crabs, which have so completely acquired the air-breathing habit that they die when immersed in water, have been derived from various marine ancestors. The molluscs offer perhaps the best examples of all of homoplasy. The pteropods, once supposed to be a most clearly defined order, are now admitted to have been derived along two lines from the opisthobranchs; the Thecosomata from *Bulla*-like forms, and the Gymnosomata from nudibranch genera. In the newest classification of the Pulmonata, the two common slugs *Arion* and *Limax* are separated from each other, the first is classed in the same family as *Helix*, and the second is made

[1] M. Laurie, "Anatomy and relation of the Eurypterida." *Trans. R. Soc. Edinburgh*, vol. xxxvii., pp. 509–528, 1893.

the type of a family by itself. Amongst the vertebrates we find numerous examples wherever we choose to look. The Teleostei are polyphyletic, and so are the ganoids; so marked does the parallelism in evolution seem to have been, that our ideas as to the mutual relationships of the two groups are in hopeless confusion. Snake-like reptiles have been derived from many families of lizards. Huxley arbitrarily selected the characters of the absence of all trace of a pectoral girdle, and of an allantoic bladder as a criterion to determine the true snakes; but it is obvious that this is a mere makeshift. Among birds, parallelism is seen everywhere, and instances of it can be found in the works of Gadow and Fürbringer.

Turning finally to the Mammalia, we find Sir William Flower writing thus of the Ruminants:—"The great difficulty which all zoologists have felt in subdividing them into natural minor groups arises from the fact that the changes in different organs (feet, skull frontal appendages, teeth, cutaneous glands, &c.) have proceeded with such apparent irregularity and absence of correlation, that the different modifications of these parts are most variously combined in different members of the group."

Such facts as these are apt to have a disheartening effect on the student of morphology. If we try to analyse the feeling of disappointment to which they give rise, we shall find, I think, that it is due to a theory we are accustomed to assume as the base of our speculations on phylogeny, with which such facts are irreconcilable. This theory, rarely explicitly stated, but everywhere postulated, holds that when one large natural group of animals was derived from another (as for instance Amphibia from Pisces), this took place by *one species* of the lower group acquiring new characters and taking to a new method of life. It is then imagined that all the species of the higher group have been derived from the modification of this single ancestral species. The view suggested, however, by the ever increasing number of cases, in which we are forced to assume a parallel development, is that a complete homology or homogeny, and a homoplasy are only after all extreme terms in a series, in which the successive terms are very closely related to each other. We seem driven to the conclusion that when a large natural group of animals was being evolved, the changed environmental conditions, which were causing the evolutional progress, acted not merely on one species but on species belonging to the same or different genera, families, or even orders, and induced similar modifications in them. The course of evolution, therefore, instead of being represented by a single trunk of a tree repeatedly branching—the typical form of the Haeckelian genealogical tree—ought rather to be pictured as a column of parallel stems with interlacing branches, like the stipe of a mushroom.

The study of systematic zoology in fact suggests, that, given a definite set of environmental conditions, any species having a given general structure exposed to them, will undergo the same change.

On the Lamarckian hypothesis this result would be attributed to the direct action of the environment; on the Darwinian view to natural selection, the only assumption which it is necessary to make, being that the small variations on which selection acts may always be trusted to occur.

All admit that the larger differences in structure which separate animals are useful, that is, are adaptive in character. Most systematists are beginning to admit that such modifications may have been effected again and again, and in despair they are taking refuge in minute peculiarities of form, pattern and arrangement, which they hope are not adaptive. This seems to me to be a futile position, the provisional acceptance of which is only rendered possible because, except in the cases where closely allied forms follow each other in immediately superposed strata, we have no means of determining the exact ancestry of a species. What we really do when we determine the structure of an animal is to unravel a series of superposed adaptations, and we class together those animals in whose structure we detect evidence of their having undergone the same series of modifications in the same order.

All similarity in structure between two animals is primarily due to similar external conditions; the longer the period of action of the same environment has been, the more complete is the likeness; and, by identity of ancestry we can only mean the extreme case in which the action of similar environmental conditions has extended for an indefinite time back into the past.

Just, therefore, as it would be a hopeless task to attempt to trace a single hypha in a mushroom stipe back to the spore from which it arose, so it appears to me is the attempt to trace several modern species back to a single original species.

The important thing to know about any hypha is its relation to the general anatomy of the plant, and especially its level on the stem; and the important thing to know about the arthropod groups is not whether they were all descended from the same species of annelid, but whether they were derived from annelid ancestors by the same series of modifications. The morphologist should aim at establishing and defining definite grades or levels of structure, and correlating these with the environmental changes which produced them.

I do not flatter myself that any of the points of view which I have endeavoured to set forth in this paper is absolutely new. Each of them will be found to have been either explicitly stated or implicitly assumed by some zoologist or other; but there is perhaps no zoologist who has not argued in a manner inconsistent with some one of the principles I have endeavoured to establish; and it seemed to me most desirable to try to give a coherent and explicit account of the principles vaguely recognised and imperfectly understood on which phylogenetic speculation is based—and such an attempt has been made in this paper.

E. W. MacBride.

NATURAL SCIENCE:

A Monthly Review of Scientific Progress.

In addition to Notes and Comments on the progress of Natural Science, brief Reviews of Current Literature, Obituary Notices, and News of Universities, Museums, and Societies, the last five numbers of this Journal comprised the following specially contributed Articles:—

No. 55, September, 1896.

I. On English Amber and Amber Generally. Part II. By Professor H. Conwentz, Ph.D. (Illustrated.)

II. What shall we do with our Local Societies? By Professor G. S. Boulger, F.L.S., F.G.S.

III. A Zoologist in Tierra del Fuego: some Account of the Swedish Expedition, 1895–1896. By Axel Ohlin, Ph.D. (With 2 Maps, Plates III. and IV.)

IV. Casual Thoughts on Museums. Part V.—Anthropology. By Sir Henry Howorth, K.C.I.E., M.P., F.R.S.

V. The Structure of the Graptolites. Part I. By Dr. Carl Wiman. (Illustrated.)

VI. Zoology since Darwin. Part I. By Professor Ludwig von Graff, Ph.D.

No. 56, October, 1896.

I. The Arctic Work of 1896. By J. W. Gregory, D.Sc., F.G.S.

II. The Structure of the Graptolites. Part II. By Dr. Carl Wiman. (Illustrated.)

III. An Introduction to the Study of Anthropoid Apes. II.—The Chimpanzee. By Arthur Keith, M.D.

IV. The Organisation of Local Science. By George Abbott, M.R.C.S.

No. 57, November, 1896.

I. The Influence of Mind in Evolution. By EHA, Author of "A Naturalist on the Prowl."

II. The Preparation and Mounting of Chalk Fossils. By Arthur W. Rowe, M.D.

III. Zoology since Darwin. Part II. By Professor Ludwig von Graff, Ph.D.

IV. An Introduction to the Study of Anthropoid Apes. III.—The Orang-Outang. By Arthur Keith, M.D.

V. The Cell, and some of its Supposed Structures. By Professor J. Bretland Farmer, M.A.

No. 58, December, 1896.

I. The Determination of Fossils (with List of Specialists).

II. Zoology since Darwin. Part III. (conclusion). By Professor Ludwig von Graff, Ph.D.

III. A Plea for Details in Comparative Anatomy. By F. G. Parsons, M.D.

IV. An Introduction to the Study of Anthropoid Apes. IV.—The Gibbon. By Arthur Keith, M.D.

V. Cunning in Animals. By W. L. Calderwood, F.R.S.E.

No. 59, January, 1897.

I. Wanted, a British Fresh-water Biological Station. By D. J. Scourfield.

II. The Position of Morphology in Zoological Science. By E. W. MacBride, B.A., B.Sc., Fellow of St. John's College, Cambridge.

III. The Earliest Known Seat of Learning in Europe. By Professor A. C. Haddon, M.A., D.Sc., M.R.I.A. (Illustrated).

IV. Cope's "Factors of Evolution." By F. A. Bather, M.A., F.G.S.

V. Wasps and Weismann. By Oswald H. Latter, M.A.

One Shilling each Number, of any Bookseller.

Annual Subscription, payable in advance to PAGE & PRATT, Ltd. (successors to Rait, Henderson & Co., Ltd.), 22 St. Andrew Street, Holborn Circus, London, E.C., Thirteen Shillings ($3.50), post free.